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Human-brown hyaena relationships and the role of mountainous environments as refuges in a postcolonial landscape

Kathryn Suzanne Williams

Abstract

Humans and brown hyaenas (*Hyaena brunnea*) frequently interact within a shifting landscape of conflict and cohabitation, yet the social and biological dimensions of these relationships, particularly in montane environments, are rarely studied. This interdisciplinary thesis investigates how attitudes and perceptions towards brown hyaenas vary between different socio-economic groups within a postcolonial framework, and how these perceptions relate to brown hyaena occupancy, density, spatial ecology, and diet. This study, which is based in and around the Soutpansberg Mountains, South Africa, uses interviews, participant observation, camera traps, GPS telemetry, and scat analysis. Members of three socio-economic groups ascribe acceptable behavioural and geographic expectations to predators. Violation of these expectations by predators strip power from people and reduce acceptance levels towards them. Regaining power and mimicking concepts of colonial domination over land are key themes in human-predator relationships. Although the brown hyaena's elusive nature and people's strong abhorrence towards leopards (*Panthera pardus*) partially protects hyaenas from attracting attention as a problem animal, anthropogenic threats still abound. The most important factor determining brown hyaena occupancy is avoiding high human activity. Despite anthropogenic risks and due to their large home ranges (95.04 km² – 169.79 km²) and dietary adaptability, brown hyaenas occupy 79% of the area surveyed. Brown hyaenas have a varied diet, which includes 48 different species. All signs suggest food acquisition through scavenging. This finding is corroborated by a high overlap with leopard diet. With lower human activity and plentiful scavenging opportunities, mountains provide a safe haven for brown hyaenas. A robust brown hyaena density between 2.56 – 3.63 per 100 km² occurs in the Soutpansberg Mountains. Recommendations to promote coexistence with hyaenas include greater education about brown hyaena ecology and their ecosystem services, non-lethal conflict mitigation, and the inclusion of people from diverse socio-economic backgrounds in conservation.

**Human-brown hyaena relationships and the role of
mountainous environments as refuges in a postcolonial
landscape**

Kathryn Suzanne Williams

Department of Anthropology

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List of Abbreviations

AIC	Akaike's Information Criterion
ANC	African National Congress
BAI	Biomass Abundance Index
BEE	Black Economic Empowerment
CFO	Corrected frequency of occurrence
GPS	Global positioning system
IUCN	International Union for Conservation of Nature
KDE	Kernel density estimate
LEDET	Limpopo Department of Economic Development, Environment, and Tourism
LoCoH	Local Convex Hulls
LUT	Land use type
MCP	Minimum Area Convex Polygon
NIMBY	Not in my backyard
PAC	Pan-Africanist Congress
PPP	Primate and Predator Project
RAI	Relative Abundance Index
SECR	Spatially Explicit Capture Recapture
T-LoCoH	Time-Local Convex Hulls
TSD	Time-scaled distance
UD	Utilisation distribution
UHF	Ultra high frequency
UNESCO	United Nations Educational, Scientific, and Cultural Organisation
UTM	Universal Transverse Mercator
VHF	Very high frequency

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For Samma

Chapter 1: Introduction

1.1. Introduction

In southern Africa, the brown hyaena (*Hyaena brunnea*), a nocturnal and cryptic carnivore, is perceived from a wide variety of contrasting perspectives. The animal is viewed both through imaginary and commonly negative constructs stemming from folklore, symbolism, and associations with witchcraft (Biesele, 1972; Glickman, 1995), and through more direct, but potentially misconceived, experiences of human-wildlife conflict through livestock losses (St John *et al.*, 2011; Thorn *et al.*, 2012). Legacies from historical inequalities between people can compound and perpetuate human-carnivore conflict (Rust *et al.*, 2016). Consequently, hyaenas face persecution from landowners because they believe that their livelihoods are at risk from depredation and from community members who are fearful of hyaenas based upon cultural associations. In addition, snaring, poisoning, and road collisions pose non-targeted threats (Collinson, 2013b; Kent, 2011; Mills and Hofer, 1998; St John *et al.*, 2011). The increasing anthropogenic risks facing brown hyaenas are poorly understood (Mills and Hofer, 1998). When compounded with a lack of data on the species' distribution, ecology, and behaviour, it is apparent that greater knowledge of this species' ecology, role in human society, and portrayal by conservationists is vital to ensure its survival. Information on human-animal interactions is essential not only to conserve African carnivores (Winterbach *et al.*, 2013) but also to improve contact between people and animals globally.

This study employs an interdisciplinary approach, which unites social and biological sciences, and specifically acknowledges and assesses the region's postcolonial climate, to understand human-brown hyaena relationships in and around the Soutpansberg Mountains, South Africa.

1.2. Human-animal relationships

The history of humanity is intertwined with the history of non-human animals, hereafter referred to as animals. No unanimous or simplistic explanation can describe how humans relate to animals. Variables which influence relationships on an individual and a species level include the animal species, the characteristics of the people involved, the rationale behind the interaction, and the geographic location (Elder *et al.*, 1998).

Relationships between humans and animals are often less indicative of an animal's characteristics and more frequently a way of examining what it means to be human (Arluke and Sanders, 1996; Knight, 2005; Mullin, 1999). Ideas and attitudes about personhood vary markedly between individuals, cultures, and contexts (Ingold, 1988), as do the myriad of factors used to distinguish human from animal (Arluke and Sanders, 1996; Berger, 2007; Elder *et al.*, 1998; Regan, 2007; Sax, 2007).

Human relations with animals lead to questions about ethics and which group's rights are more important. If an anthropocentric point of view is applied to relationships, it is often assumed that sacrificing animals is acceptable if the process benefits humanity, but this is fraught with subjectivity (Regan, 1986). Animal rights is a highly contested area, with some animal rights advocates hankering for complete species equality (e.g. Regan, 1986) while many people argue for a more productive approach (Singer, 1974). The debate boils down to the dynamic question of how an animal is defined, which is a non-static point. Regan (2007) suggests that there are two solutions to this problem: the first is to delineate which qualities define a human, thus imbuing only those individuals who meet certain criteria with rights; the second is to broaden the definition to allow more individuals rights. In the first instance, some humans would be excluded from rights and in the second, more animals would be allowed rights (Regan, 2007). As concluded by Anderson (2004), there are no easy answers in these types of debates.

Human-animal relations are developed either with a known individual, or with a generalised species or a specific group of animals in mind. Collective terms such as

animals, species, and herds are commonly used when speaking about animals and the individual is often overlooked in academic or conservation discussions unless domesticated animals are involved (Bear, 2011; Carrithers *et al.*, 2011; Knight, 2005; van Dooren, 2010). In this context, the word species is synonymous to the term person and one human being is therefore viewed as equally important as a biological species (Carrithers *et al.*, 2011).

Animals are integral to human survival for a wide variety of reasons. Functionally, animals provide people with food, raw materials, labour, companionship, and entertainment (Shanklin, 1985). Animals also provide important ecosystem services (Ćirović *et al.*, 2016; DeVault *et al.*, 2003; Ripple *et al.*, 2014). Dependency on the utilisation of animals affected the development of domestication and farming practices, events that substantially influenced human history (Shanklin, 1985). Domestication is described as the lynchpin in man's rise above nature and animals (Ingold, 2000, p. 64; Power, 2012). Anthropocentric power relations between humans and animals, which centre around the belief that human beings are more important than other animal species, are a reoccurring and important theme when examining human-animal interactions (Ritvo, 1995).

Attitudes towards animals vary between species based upon their perceived usefulness. The most popular animals in a public survey featuring 33 very different species were large mammals, especially primates and companion animals, while the least popular were biting invertebrates (Driscoll, 1995). Animals such as the common mussel (*Mytilus edulis*) are at a disadvantage due to both a lack of charisma and similarities with people (Carrithers *et al.*, 2011).

Social structures are responsible for the complexity of human-animal relations as an animal is always a social and cultural being (Marvin, 2005). Animals play an important symbolic and metaphorical role in folklore, divinity, satire, and politics (Sax, 2007). The way people perceive animals directly impacts how they act towards them (Marchini and Macdonald, 2012; Marker *et al.*, 2003a; Mateo-Tomás *et al.*, 2012), although factors such as economic incentives can also influence behaviour (Liu *et al.*, 2011).

Perceptions of animals shift across time and space, as do responses to them. The way animals are viewed at a particular time is dependent on context, feelings, and motives (Arluke and Sanders, 1996; Lawrence, 2003). Ideas about animals are often based on social constructions rather than direct involvement (Gullo *et al.*, 1998). Social constructions, which develop from personal opinions, can perpetuate through societal and institutional avenues to create a mediated characterisation of an animal, which then becomes widely adopted and attitude-defining (Gullo *et al.*, 1998).

Relationships between humans and animals are constantly changing. In rural Africa, as in the rest of the world, many people are dependent upon their environment for survival and although people generally do not make a conscious effort to harm the balance of nature, sustainability is seldom prioritised (Adams and McShane, 1996). However, a kinship between hunter and animal is traditionally found in rural Africa and killing is steeped in ritual practices and respect (Morris, 1998, 2000a). The animal, which is considered a spiritual equal, sacrifices itself to be killed if the hunter is spiritually and mentally ready (Morris, 2000a). In Malawi, this close relationship between people and nature diminished with the spread of subsistence farming. Wild animals pose a risk to agricultural success through predation and damage to crops and this has motivated a change in how wild animals are perceived (Morris, 1998).

Finally, social perceptions of human-animal relationships require scrutiny. In many cases, perceptions of “traditional people” living in ‘perfect balance’ with nature are not as one-dimensional as they initially appear, illustrating the complexity of humans’ relationships with nature (Ellen, 1986; Milton, 1996, p. 112; Strang, 2005). For example, although portrayals of Native Americans often illustrate a sustainable and harmonious relationship with nature, this group was guilty of deforestation and elimination of North American buffalo (*Bison bison*) (Ellen, 1986).

1.3. Human-carnivore relationships

1.3.1. Why conserve carnivores?

Species are becoming extinct at an increasingly accelerated rate, suggesting that the planet may be experiencing its sixth mass extinction (Barnosky *et al.*, 2011). Megafauna are facing severe declines, with 59% of the world's largest carnivores and 60% of the world's largest herbivores listed as threatened with extinction on the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species (Ripple *et al.*, 2016). Careful conservation is required to counteract this trend and it will be necessary to decide which species to invest in saving (Gittleman *et al.*, 2001). Intuitively, it is natural to select species that are generally well liked. Carnivores produce divided public opinion and are therefore a special case in wildlife management. They are often valued at a global scale for their role in biodiversity and their charismatic nature, but on a local level they may be disliked due to the conflict and financial losses they impose (Dickman *et al.*, 2011). Protecting these species may involve finding a way to transfer internationally perceived value to a local level (Dickman *et al.*, 2011). Additionally, predator species can be revered and hated within the same geographic space, which makes conservation management and public engagement especially challenging (Knight, 2000a). In Japan, people are scared of bears and associate them with aggressive behaviour and man-eating (Knight, 2000a). Conflict with humans in forestry plantations where bears strip bark or on farms where they take or vandalise crops increases negative attitudes and rallies support for culling (Knight, 2000a). At the same time, bears also are viewed sympathetically and admired. The public image of a bear (or a teddy bear) 'standing up' on two feet like a human and caring for its infants invokes anthropomorphic representations (Knight, 2000a).

Since carnivores straddle a fine line between love and hatred, overall costs and benefits of their conservation must be seriously considered (Gittleman *et al.*, 2001). Carnivores are expensive to study and conserve because their secretive nature often requires valuable equipment such as global positioning system (GPS) collars, helicopters, and lab tests (Gittleman *et al.*, 2001). These costs need to be measured

against the benefits carnivores provide through the provision of vital ecosystem services (Ćirović *et al.*, 2016; DeVault *et al.*, 2003; Ripple *et al.*, 2014).

Large carnivores fit within many or all ecological classifications (Gittleman *et al.*, 2001; Linnell *et al.*, 2000). They are indicator species, which can therefore demonstrate environmental damage. They are keystone species that play an important role in ecosystem stability and maintaining prey numbers (Mills, 2005). On islands devoid of vertebrate predators, densities of prey species were elevated by 10 to 100 times compared to similar systems on the mainland which included predators (Terborgh *et al.*, 2001). In addition, vegetation levels were severely decreased as a result of overly high herbivorous activity (Terborgh *et al.*, 2001). Due to their large home ranges, carnivores are umbrella species and thus can protect other species through their own conservation. Their popularity and place in the human imagination makes them flagship species (Gittleman *et al.*, 2001). Many carnivores are also vulnerable species that face extinction (Gittleman *et al.*, 2001).

However, the value of these ecological categories is sometimes overstated in the context of large carnivores. In Scandinavian boreal forests, gaining support for large carnivores such as the wolf (*Canis lupus*), the Eurasian lynx (*Lynx lynx*), and the brown bear (*Ursus arctos*) as flagship species is not possible due to conflict with farmers and negative perceptions (Linnell *et al.*, 2000). These predators have little use as indicator species because intensive forestry practices artificially increase the prey base and therefore improve carnivore success, rather than diminish it. Yet these same forestry practices are often detrimental for some of the most vulnerable species – a fact not reflected in predator numbers (Linnell *et al.*, 2000).

Species vulnerability must be considered when planning conservation measures. As the human population rises, carnivore numbers are expected to decline (Woodroffe, 2000). With an increasing human population, a carnivore's biological traits largely define its extinction risk (Cardillo *et al.*, 2004). Some species such as foxes, coyotes (*Canis latrans*), and raccoons (*Procyon lotor*) are plentiful and adaptable, however many larger species are extremely vulnerable to extinction due to narrow geographic ranges, small and isolated populations, low genetic diversity, large home ranges,

specialised niche requirements, and threats posed by people (Gittleman *et al.*, 2001; Sillero-Zubiri and Laurenson, 2001). Winterbach *et al.* (2013) identified 14 key factors affecting carnivore conservation and suggests that as all factors are interrelated, a connected and multifaceted approach is required when implementing carnivore conservation strategies.

1.3.2. Human-wildlife conflict

Human relationships with animals are largely positive from an anthropological point of view due to the material or emotional benefits humans derive from animals. However, with human-wildlife conflict the relationship is negative for both parties (Thirgood *et al.*, 2005).

Human-wildlife conflict “occurs when the needs and behaviour of wildlife impact negatively on the goals of humans or when the goals of humans negatively impact on the needs of wildlife” (Madden, 2004, p. 248). It is increasingly acknowledged that socio-economic issues often spark human-wildlife conflict, thus human-wildlife conflict regularly masks human-human conflict (Dickman, 2010; Hill, 2015; Madden, 2004; Madden and McQuinn, 2014; Marshall *et al.*, 2007; Peterson *et al.*, 2010; Redpath *et al.*, 2013). The term ‘human-wildlife conflict’ is misleading as it does not acknowledge underlying socio-economic disputes, anthropomorphises animals as conscious antagonists, and it can divert responses away from core issues (Hill, 2015; Peterson *et al.*, 2010). Alternative terms such as ‘human-human conflict’, ‘conservation conflict’, and ‘human-wildlife interaction’ have been suggested but have not been adopted widely (Hill, 2015). Despite the ambiguity of the term ‘human-wildlife conflict’, it is used hereafter following the definition given by Madden (2004), as it is required to specifically denote negative experiences.

Human-wildlife conflict is a global problem threatening human physical wellbeing and economic livelihoods as well as the animals involved (Knight, 2000b; Thirgood *et al.*, 2005). This growing problem is provoked by both biological and socio-political agendas (Treves and Karanth, 2003), hence an interdisciplinary approach to combat the

problem is required (Clark *et al.*, 2001; Madden and McQuinn, 2014). Although financial losses can spur greater conflict, social and environmental factors have a larger detrimental impact in some circumstances (Thorn *et al.*, 2012). As well as direct costs, conflict can instigate indirect costs such as the time spent to defend resources and associated loss of income (Thirgood *et al.*, 2005). Conflict can take many forms, including crop raiding by herbivores such as elephants, monkeys, or pigs (de Motts and Hoon, 2012; Linkie *et al.*, 2007a; Priston *et al.*, 2012), human fatalities and injuries (Liu *et al.*, 2011; Morris, 2000b; Packer *et al.*, 2005; Treves and Naughton-Treves, 1999), transmission of disease, and livestock or game losses from carnivores (Marker *et al.*, 2003a; Ogada *et al.*, 2003; Thorn *et al.*, 2012). Many of these adverse outcomes may be compounded and occur simultaneously (Liu *et al.*, 2011).

A survey of 481 households outside of the Serengeti National Park in Tanzania found that livestock lost to predation equates to an average annual financial loss of 19.2% (US \$26.8) of a family's yearly cash income (Holmern *et al.*, 2007). Loss of livestock not only threatens people's immediate needs such as food, but also endangers the cultural and symbolic balance of communities because of cattle's role in bridewealth, power relations, trade, and spirituality (Evans-Pritchard, 1940; Ferguson, 1985).

Large carnivores are particularly vulnerable to conflict due to their large home ranges and dietary requirements (Frank *et al.*, 2005; Sillero-Zubiri and Laurenson, 2001). A growing human population and higher economic demands on land transforms once wild habitats to modified spaces in human-dominated landscapes, reduces the number of wild prey, and increases the propensity for carnivore conflict (Lambert *et al.*, 2006). People living alongside large carnivores are often quick to blame these animals for livestock losses although other agents such as disease might be responsible (Dar *et al.*, 2009). In a survey of 99 landowners in the North West Province, South Africa, 149 predation incidents were recorded and of these 41% were attributed to jackals, 20% to caracals (*Caracal caracal*), 15% to leopards (*Panthera pardus*), 12% to brown hyaenas, 7% to cheetahs (*Acinonyx jubatus*), 3% to spotted hyaenas (*Crocuta crocuta*), and one attack to serval (*Leptailurus serval*) (Thorn *et al.*, 2012). Culpability was mainly deduced from spoor and feeding habits, but actual observations also contributed. Sixteen per cent of interviewees inferred blame with no

supporting evidence (Thorn *et al.*, 2012). In Ghanzi, Botswana, farmers are generally supportive of conservation, but show little support for predators which threaten their livestock (Kent, 2011). Similarly, despite a generally positive feeling towards large carnivore conservation, negative views towards lions (*Panthera leo*), particularly those perceived as a threat to humans and livestock, is common among people living in areas bordering Kruger National Park, South Africa (Lagendijk and Gusset, 2008).

Animals in conflict with people often have negative reputations and may be associated with supernatural powers such as shapeshifting (Knight, 2000b). Wolves are commonly believed to transcend the human-animal boundary (Lindquist, 2000). These ideas can ignite further fear and rouse suspicion as they bring the wild predator into the human shell (Knight, 2000b).

The intensity and frequency of conflict can vary throughout seasons. In a farming community near to the Maasai Mara National Reserve, Kenya, depredation by spotted hyaenas fluctuates in relation to rainfall and natural prey availability (Kolowski and Holekamp, 2006).

Retaliatory behaviour against animals blamed for livestock losses and crop damage is common (Ikanda and Packer, 2008; Kissui, 2008; Ogada *et al.*, 2003; Romañach *et al.*, 2011), especially amongst people with negative attitudes towards problem animals or experiencing regular losses (Romañach *et al.*, 2011). In Spain, poisoning birds of prey and mammalian carnivores is motivated by perceived risk of predation (Mateo-Tomás *et al.*, 2012). Retaliatory killings of jaguars (*Panthera onca*) can be predicted not only from the threats they pose to livestock but also from fears, personal motivations, and other barriers such as low education or political unrest (Marchini and Macdonald, 2012).

1.3.3. Approaches in carnivore conservation

Non-lethal methods to mitigate human-carnivore conflict include kraaling livestock, building enclosures from hardy natural materials, and using guard dogs (Bauer *et al.*,

2010; Frank *et al.*, 2005; Lagendijk and Gusset, 2008; Ogada *et al.*, 2003). Instances of depredation are most significantly reduced when livestock is monitored by a herder in the day and enclosed in a kraal at night (Ogada *et al.*, 2003; Woodroffe *et al.*, 2007). However, there is not always a simple solution that protects livestock from all types of predators. Kraals made of local bush materials are more likely to be attacked by spotted hyaenas than ones constructed of pole materials, while the opposite is true regarding leopard attacks (Kolowski and Holekamp, 2006).

Promoting sustainable solutions to human-wildlife conflict can be challenging if communities do not value predator species. This is especially true for animals like hyaenas which are generally thought to be of little use to humans (Kruuk, 1972). Some conservationists and economists claim that placing a price tag on the value of animals is one of the best approaches to entice people to preserve wildlife (Büscher, 2010; MacMillan and Leader-Williams, 2008; Norton, 2000). In Africa, wild animals are bestowed with a financial value through capital-gaining practices such as ecotourism, game ranching, or trophy hunting (Adams and McShane, 1996; Chardonnet *et al.*, 2002). Profits generated from wildlife often improve attitudes towards animals (Gadd, 2005). Some animals also have consumptive value as a source of *bushmeat*¹ or traditional medicine (Chardonnet *et al.*, 2010; Whiting *et al.*, 2011). Other aspects of Africans' relations with animals such as the desire to preserve national heritage and the socio-cultural importance of wildlife are also important when contemplating value (Adams and McShane, 1996; Chardonnet *et al.*, 2010). Nature's cultural worth is not always compatible with economic incentives in conservation (MacMillan and Phillip, 2010) and nor are arguments about preserving nature for its intrinsic value (Norton, 2000), but it is essential that material benefits of species do not overshadow cultural

¹ Bushmeat hunting is described as the hunting of wildlife for food (Nielsen, 2006), specifically through illegal acquisition (Lindsey *et al.*, 2013a). The term 'bushmeat' has problematic connotations because it is primarily associated with African practices and does not express the global nature of illegal wildlife acquisition and trade (Milner-Gulland and Bennett, 2003). Consequently, the IUCN utilises the term 'wild meat' to overcome this barrier (Milner-Gulland and Bennett, 2003). Within this thesis, I describe meat from wild animals as 'bushmeat' rather than 'wild meat' because it adheres to the terminology used at my study site and by my research participants.

and intrinsic values (Robinson and Sasu, 2013). Losses incurred by animals through human-wildlife conflict are referred to as counter- or anti-values (Chardonnet *et al.*, 2010, p. 16). Despite comparative difficulties, financial values, cultural values, and intrinsic benefits should be weighed against financial losses carnivores impose on farmers when responding to human-wildlife conflict (MacMillan and Leader-Williams, 2008; Thorn *et al.*, 2012).

Well-managed formally protected areas are necessary to preserve high biodiversity levels and predator population densities in developing countries (Balme *et al.*, 2009b; Loveridge *et al.*, 2010; Naughton-Treves *et al.*, 2005). However, only a small proportion of land in Africa is designated for formal protection² (Deguignet *et al.*, 2014; Trimble and Van Aarde, 2014). These areas cannot always meet spatial requirements and provide wildlife corridors required by large mammals (Burkey, 1995; Mills, 2005; Woodroffe and Ginsberg, 1998) or include large enough areas to fully encapsulate biodiversity hotspots (Soulé and Sanjayan, 1998). Biodiversity and species-specific protection on non-protected land is therefore essential for conservation and to counter increasing climatic and human-induced pressures on a global scale (Burkey, 1995; Mora and Sale, 2011; Trimble and Van Aarde, 2014). Private land is especially important for the survival of brown hyaenas (Kent and Hill, 2013; Maude and Mills, 2005; Thorn *et al.*, 2012), which are reliant on sizeable areas where competitor species are largely absent (Mills, 1984; Mills and Mills, 1982). African national parks often house healthy populations of dominant competitors such as spotted hyaenas and lions which restrict the success of subordinate predators like African wild dogs (*Lycaon pictus*), brown hyaenas, and cheetahs (Marker *et al.*, 2010; Mills and Gorman, 1997).

² Approximately 14.7% of the land in Africa is protected for conservation (Deguignet *et al.*, 2014). State owned conservation areas account for 7% of South Africa's total land area (Walker and Dubb, 2012).

1.4. Brown hyaenas

There are four species of hyaenas in the family Hyaenidae: the striped hyaena (*Hyaena hyaena*), the brown hyaena, the spotted hyaena, and the aardwolf (*Proteles cristata*) (Mills and Hofer, 1998). The Hyaenidae family is more closely related to felines than canids (Holekamp, 2016). Their closest living relatives are the fossa (*Cryptoprocta ferox*) and mongooses (Holekamp, 2016). The striped hyaena, spotted hyaena, and brown hyaena belong to the sub-family, Hyaeninae, and the aardwolf, which has five digits rather than four on its forelegs and dentition adapted for insectivory, is classified within its own sub-family, Protelinae (Skinner and Chimimba, 2005).

Brown hyaenas are visually distinctive due to their brown shaggy pelage, their white striped legs and their long pointed ears. Adults weigh about 40 kilograms and stand at approximately 0.79 metres at the shoulder (Smithers, 1986). There is very little difference in appearance or size between males and females (Mills and Hofer, 1998; Owens and Owens, 1996). Brown hyaenas have a catholic diet (Burgener and Gusset, 2003; Maude and Mills, 2005; Mills and Mills, 1978) and they are primarily scavengers of mammal remains (Maddock, 1993; Mills, 1982a).

Brown hyaenas are nocturnal and active for 80% of the period between 18:00 and 6:00 (Mills, 1984). Brown hyaenas have a peak in activity in the early evening, approximately between 19:30 and 00:00, a resting period, and then another peak in activity between 02:30 and 06:00 (Owens and Owens, 1978).

Although 65% of brown hyaenas live in mixed sex clans (Mills, 1983) of between four to 14 individuals (Mills, 1982b), they are solitary foragers that spend much of their time independently (Owens and Owens, 1996; Skinner and Chimimba, 2005). A clan is generally composed of one dominant male and a dominant unrelated female (Knowles *et al.*, 2009), several additional females, natal male adults, subadults, and cubs (Mills, 1982b; Owens and Owens, 1996). A small subsection of brown hyaenas are solitary nomads that do not identify with a clan or sub-adults that are seeking a clan (Mills, 1982c; Mills, 1983). Brown hyaena clans occupy communal den sites that can be

located in caves or holes in the ground (Mills and Hofer, 1998; Skinner, 1976) (Figure 1.1).



Figure 1.1 Active brown hyaena dens in Limpopo Province, South Africa. Both sites have a substantial amount of faeces and prey remains within a 50 m radius of the entrance. a. A cave used as a brown hyaena den in the western Soutpansberg Mountains. b. A hole in the ground used as a brown hyaena den on the flatlands north of the Soutpansberg Mountains.

Clans mark their territory using olfactory anal pastings and latrines, and defend their territory through aggression (du Plessis Bothma and Walker, 1999). Due to the high frequency of pastings around the edge of a territory, it is unlikely that a foreign individual will be able to enter another clan's territory unaware (du Plessis Bothma

and Walker, 1999). Meetings between members of different groups are consequently fairly rare (Mills, 1983).

Brown hyaenas have the smallest geographic range of all hyaena species (Mills and Hofer, 1998). Their distribution is confined to southern Africa and especially the region's drier western areas (Mills and Hofer, 1998; Smithers, 1986) (Figure 1.2). Brown hyaenas occur in parts of Angola, Botswana, Namibia, South Africa, and Zimbabwe (Wiesel, 2015). The species utilises a wide variety of habitat types including desert, coastal areas, semi-desert, open scrub, and open woodland savannah (Mills and Hofer, 1998). The brown hyaena's range has diminished since the eighteenth-century when animals were recorded as far south as South Africa's Cape Province (Stuart *et al.*, 1985). Recent research in the former Transvaal Province³, South Africa, shows that brown hyaenas occupy a larger and less fragmented range there than previously imagined and are therefore more resilient to anthropogenic threats than formerly believed (Thorn *et al.*, 2011b). However, little research to date has been undertaken on which factors influence brown hyaena occupancy on private land.

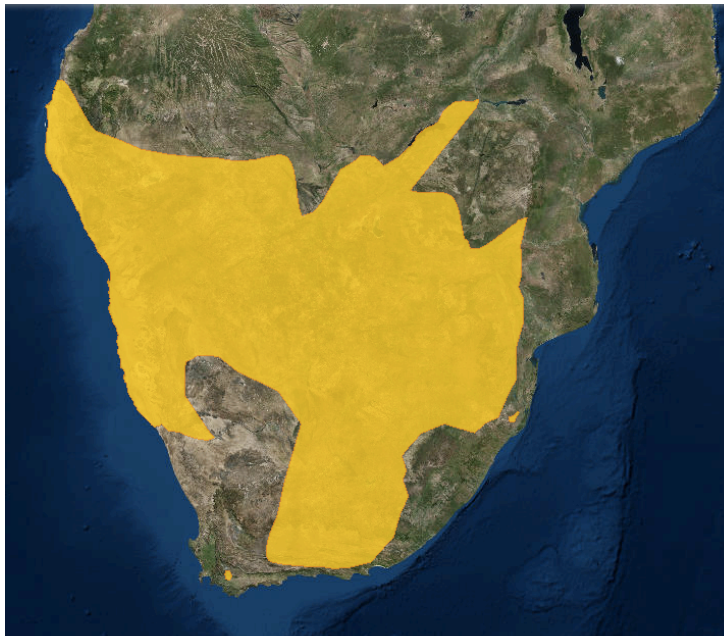


Figure 1.2 Map of southern Africa showing brown hyaena global distribution as defined by the IUCN Red List of Threatened Species (Wiesel, 2015). Yellow shading indicates presence of brown hyaenas.

³ The Transvaal included all or part of the modern day provinces of Limpopo, North West, Mpumalanga, and Gauteng.

Studies on brown hyaenas have mainly focused on populations living in or near the Kalahari in Botswana and South Africa (Adler, 1996; Knowles *et al.*, 2009; Maude and Mills, 2005; Mills, 1982a; Owens and Owens, 1978) and coastal Namibia (Kuhn *et al.*, 2008; Skinner and Van Aarde, 1981; Wiesel, 2006). However in recent years, research on brown hyaenas in South Africa has begun to receive more attention (Richmond-Coggan, 2014; Thorn *et al.*, 2011a; Welch and Parker, 2016; Welch *et al.*, 2016). Still few data exist on the species in Limpopo Province, South Africa, despite the importance of the area as a population source (Mills and Hofer, 1998; Richmond-Coggan, 2014).

It is estimated that there are between 5,000 and 8,000 brown hyaenas remaining world-wide (Mills and Hofer, 1998). South Africa is home to one of the largest populations of brown hyaenas in the world with an estimated 1,007 animals (95% confidence interval between 31 – 2,316) (Thorn, 2009). The brown hyaena population in the former Transvaal area of South Africa, where this study is located, is estimated at 1,000 individuals with a minimum estimate of 500 and a maximum estimate of 1,500 (Mills and Hofer, 1998). Similarities between population estimates nationally and in the Transvaal, illustrate inconsistency in information about the species' demography and highlight that more detailed and contemporary information on brown hyaena population and distribution in South Africa is clearly required.

1.4.1. Threats to brown hyaenas

The brown hyaena is classified as near threatened by the IUCN Red List of Threatened Species because the population is estimated at below 10,000 individuals and due to the deliberate persecution of the species (Wiesel, 2015). Anthropogenic threats such as poisoning, trapping, hunting, and vehicle collisions are causing the brown hyaena population to decline (Mills and Hofer, 1998; Wiesel, 2015). Despite these threats, brown hyaenas can adapt well to areas with human activity and thrive on agricultural land (Kent and Hill, 2013; Mills and Hofer, 1998; Skinner, 1976).

Brown hyaenas pose a minor threat to livestock. Although brown hyaenas hunt prey, this action only constitutes about 5% of their dietary intake (Maude and Mills, 2005; Mills, 1984; Owens and Owens, 1978). Predation on small stock such as goats (*Capra hircus*), sheep (*Ovis aries*), and chickens (*Gallus domesticus*) is primarily attributed to one anomalous individual rather than wider populations (Skinner and Chimimba, 2005; Skinner, 1976). Cattle was detected in the scats of brown hyaenas living in farmland areas of Botswana, although there is little evidence from observations of collared individuals there to suggest that brown hyaenas generally kill cattle (Maude and Mills, 2005). It is more probable that they scavenge upon carcasses (Maude and Mills, 2005). Rare exceptions to this trend have been recorded. In a study based in Mpumalanga Province, South Africa, brown hyaenas were responsible for 48% of attributable livestock losses and leopards accounted for the remaining 52% (Van As, 2012).

In Limpopo Province, the brown hyaena is considered a protected species and it is illegal to kill a brown hyaena without a problem animal permit (Department of Environmental Affairs and Tourism, 2007). Nevertheless, perceived instead of actual conflict drives retributive killings (Marker *et al.*, 2003a; Mishra, 1997). Consequently, regardless of the reality, many farmers blame brown hyaenas for depredation and retaliate with poisoning, shooting, or trapping (Mills and Hofer, 1998).

1.5. Research aims and objectives

Aim 1: Discover how people from different cultural and socio-economic backgrounds living in and around the Soutpansberg Mountains relate to brown hyaenas.

Objectives:

- Investigate how perceptions of and attitudes towards brown hyaenas vary between people from different backgrounds and cultures.
- Explore direct and indirect experiences with brown hyaenas.
- Determine the geographical spaces brown hyaenas are perceived to occupy.

Aim 2: Discover how historical and current disparities in power between groups affect human-brown hyaena relationships.

Objectives:

- Investigate how legacies of colonialism and apartheid affect how people from different cultural groups interact with and perceive wildlife today.

Aim 3: Establish the occupancy, population density, ranging behaviour, and dietary preferences of brown hyaenas in mountainous and low-lying environments. Compare the results of the ecological investigation with perspectives presented by people.

Objectives:

- Determine the population density of brown hyaenas in the Soutpansberg Mountains.
- Determine which factors affect brown hyaena occupancy.
- Determine the home range size of adult brown hyaenas and which land use types they frequent.
- Determine dietary preferences and the extent of livestock consumption by brown hyaenas.

Aim 4: Make suggestions for improving human-brown hyaena relationships and conserving carnivores.

Objectives:

- Combine social and biological learning to design conservation strategies, which are shaped around the diversity of groups present in the area.

1.6. Theoretical considerations

This thesis' interdisciplinary approach requires an eclectic theoretical framework. I examine concepts from across the social and biological disciplines to analyse human-brown hyaena relationships in and around the Soutpansberg Mountains, South Africa.

By drawing upon a rich body of literature, this research acts as a case study with broader intellectual significance for the fields of conservation management and non-human anthropology.

A postcolonial framework runs throughout the thesis and provides a conduit for interpreting results. Postcolonialism investigates how colonial power structures impact upon people and places after the denouement of colonialism (Sharp, 2009, p. 4). Within this thesis, I expand this definition to include effects upon animals as well.

Literature on human-animal relationships is essential in interpreting how people at my study site relate to hyaenas. Works that examine hidden societal components underpinning relationships with animals are especially pertinent (e.g. Arluke and Sanders, 1996; Mullin, 1999). In recent years, this theory has gained momentum within the more biologically grounded exploration of human-wildlife conflict (e.g. Dickman, 2010; Hill, 2015; Madden, 2004; Madden and McQuinn, 2014; Marshall *et al.*, 2007; Peterson *et al.*, 2010; Redpath *et al.*, 2013).

Perceptions about animals do not always match biological realities. The disparity between ‘real’ and ‘imagined’ animals is integral to this thesis. Glickman (1995) and Kruuk (2002) examine hyaenas’ negative stereotyping and comment about the inaccuracies of such perceptions in relation to their cultural significance. These texts provide a platform to examine perceptions and realities of brown hyaenas and to use brown hyaenas as a focal species to decipher how attitudes and perceptions affect the entire large carnivore guild.

Theories pertaining to power structures and control are vital to my understanding of human-brown hyaena relationships. Within this sphere, I explore concepts of masculinity, autonomy, bravado, and domestication. I draw upon the emerging literature pertaining to how historical inequalities influence the way predators are perceived and treated in southern Africa (Rust and Taylor, 2016; Rust *et al.*, 2016). Rust’s examples from Namibia (Rust and Taylor, 2016; Rust *et al.*, 2016) provide a foundation for exploring the effects of colonisation and apartheid on relations with brown hyaenas and other large predators in Limpopo Province, South Africa.

Biological and ecological theories support my interpretation of data on brown hyaena occupancy, density, ranging, and diet. Carnivore density is affected by the availability of prey (Carbone and Gittleman, 2002) and prey biomass (Kruuk and Parish, 1982; Van Orsdol *et al.*, 1985). The optimal foraging theory states that prey availability has a direct correlation on prey consumption by predators (Brown, 1988; Krebs, 1978). A predator's diet includes a wider variety of species in areas where productivity is lower (Krebs, 1978). This theory is also applicable when applied to scavenging behaviour (Maude, 2005).

Predator density and distribution is influenced by the presence of competitor species (Carbone and Gittleman, 2002; Caro and Stoner, 2003; Creel *et al.*, 2001). Threats of death or injury resulting from interspecific competition can provoke spatial partitioning between members of the carnivore guild. Higher densities of spotted hyaenas, a more dominant predator, affect brown hyaena ranging behaviour (Mills and Mills, 1982). Regardless of the feeding potential an area offers, if spotted hyaena density is high, the area is avoided by brown hyaenas (Mills and Mills, 1982). Coyotes and grey foxes (*Urocyon cinereoargenteus*) actively partition the areas which they occupy with the more dominant coyote utilising a wider range of habitats and exploiting more food sources than the grey fox, thereby reducing competition pressure within the same national parks (Fedriani *et al.*, 2000). Conversely, the presence of apex predators can be conducive to hosting higher densities of brown hyaenas due to the scavenging opportunities provided by the presence of large predators (Yarnell *et al.*, 2013).

Apex predators play an important role in regulating populations of smaller mesopredators. When the population of an apex predator declines, mesopredator populations often increase through the mesopredator release effect (Crooks and Soulé, 1999). In the absence of apex predators, smaller predators gain access to richer and more varied food sources free from the dangers of competition (Crooks and Soulé, 1999). Mesopredators often specialise in smaller prey (Ritchie and Johnson, 2009). As larger herbivores become more infrequently consumed, this causes a surge in their populations and may result in overgrazing (Ripple and Beschta, 2012). Therefore, the

loss of an apex predator can create a trophic cascade affecting all parts of the ecosystem, including plant communities (Estes *et al.*, 2011; Terborgh *et al.*, 2001; Trewby *et al.*, 2008).

Home range size in social carnivores is defined by resource availability rather than population constraints, as epitomised through the resource dispersion hypothesis (Macdonald, 1983). Larger territories represent a wider distribution of food patches (Macdonald, 1983). In carnivore communities, food availability also influences group size, irrespective of territory size (Macdonald, 1983). More individuals residing in larger groups can be supported in areas with greater food resources (Mills, 1984). As human activity alters the availability of resources and provides alternative food patches for carnivores, the resource dispersion hypothesis may acquire new implications for conservation and population ecology (Hidalgo-Mihart *et al.*, 2004). For example, a group of coyotes living in a landfill have a smaller home range and a larger group size than coyotes residing in an adjacent forest with no access to artificial food sources (Hidalgo-Mihart *et al.*, 2004). The home range of a clan of spotted hyaenas living near human infrastructure within Kruger National Park is smaller than a comparative group independent from human habitation (Belton *et al.*, 2016). This finding was attributed to alterations in the spatial distribution of food by humans (Belton *et al.*, 2016).

1.7. Thesis structure

Chapter 2 explains the study's interdisciplinary approach and offers a broad background on the study site and the wider area. In addition, a historical context which contextualises this thesis' postcolonial structure is provided. Chapter 3 provides a detailed description of the interviewee groups and examines respondents' experiences and perceptions of brown hyaenas. Chapter 4 employs a postcolonial framework to expand upon the social science data. This chapter investigates how various power structures monopolise relationships between humans and carnivores and impact upon actions. Chapter 5 uses camera trap data to determine brown hyaena density and factors affecting occupancy. Chapter 6 explores home ranges, daily movement patterns, and the exploitation of different land use types by GPS collared

brown hyaenas. Brown hyaena diet is discussed in Chapter 7. This chapter examines species identified and their frequency of occurrence within brown hyaenas scats in relation to prey abundance, leopard diet, and commercial hunting. Finally, Chapter 8 concludes the thesis by summarising key findings in relation to the objectives and suggesting conservation strategies and recommendations for further research.

Chapter 2: Methods and historical context

2.1. A multi-method interdisciplinary approach

Conservation biology developed in the 1980s to respond to the ‘extinction crisis’ (Noss, 1999). Tackling this global dilemma was considered too complex for a single discipline approach, hence the development of a new interdisciplinary arena of study. Interdisciplinary approaches are recognised as the best way to examine complicated questions which extend beyond the boundaries of a single discipline (Milgroom *et al.*, 2014; Repko, 2012). Effective wildlife conservation requires an understanding of numerous disciplines with a special emphasis on the social and biological sciences (Adams and McShane, 1996; Bauer *et al.*, 2010; Yirga Abay *et al.*, 2011). Interdisciplinary studies are increasingly acknowledged as a pre-eminent approach to conduct well-rounded research on environmental topics and to develop sustainable and accessible conservation strategies (Allendorf *et al.*, 2012; Clark *et al.*, 2001; West and Brockington, 2006).

Despite the need for a balanced approach, integration is not always equal across interdisciplinary projects with many conservation biologists arguing that biology is the core discipline and human dimensions should be considered secondarily (Newing, 2010). Social scientists report feeling demoralised, undervalued, and outnumbered in some interdisciplinary conservation projects (Marzano *et al.*, 2006; Mascia *et al.*, 2003). The social sciences are often neglected in graduate training programmes with a conservation focus (Newing, 2010; Noss, 1999).

In recent years, research has begun to successfully incorporate multiple methods but is often criticised by integrationist interdisciplinarians for retaining a piecemeal approach when presenting and discussing results (Repko, 2012). This outcome is defined as multidisciplinary rather than interdisciplinary (Repko, 2012). The terms are often used interchangeably and hence incorrectly. Multidisciplinary studies employ multiple disciplines alongside each other but methods and results remain clearly

discernable as separate areas of study. Interdisciplinary studies meld different disciplines across all levels to create a synthesised output that is independent of a single area of study (Pooley *et al.*, 2013; Repko, 2012).

Biological and social methods and their results are sometimes considered independently and deliberated jointly only at the conclusion, maintaining a strong division between the sciences and adhering to a multidisciplinary approach rather than achieving interdisciplinarity (Fox *et al.*, 2006; Walker, 2005b). Collaboration from the onset is highly recommended to improve the effectiveness of conservation actions (Campbell, 2005; Fox *et al.*, 2006).

I used an interdisciplinary approach to address complex questions about relationships between humans and brown hyaenas and to recommend appropriate conservation practices. Interdisciplinary projects often unite academic collaborators from varied disciplines to solve problems (Strang, 2009). However, within this research I assumed the role of the social and the biological scientist. By adopting a singular ‘multilingual’ position I overcame some of the challenges of multi-partner collaboration such as recruiting an appropriate team and clarifying power relations within the team. Some conceptional challenges remained (e.g. disciplinary prejudices and interdisciplinary communication) and I attempted to self-regulate my work and incorporate approaches suggested for successful interdisciplinary projects (Campbell, 2005; Marzano *et al.*, 2006; Pooley *et al.*, 2013).

Within each chapter and across all of my research aims, I considered all relevant social and biological methods together to achieve a greater degree of interdisciplinarity. In some cases, I discussed results from multiple methodologies simultaneously in relation to a chapter’s central theme. This thesis is mostly written in present tense following convention in the social sciences. Although this is uncommon in the biological sciences, this interdisciplinary thesis necessitates a different approach.

2.2. Data collection

I primarily conducted research over a two-year period between February 2013 and February 2015. Brown hyaena scat collection commenced in July 2011 when I began working at Lajuma Research Centre for Dr Russell Hill's Primate and Predator Project (PPP) and concluded in April 2016. The extended scat collection period was required to accumulate a large enough dataset across multiple seasons. My second spatially explicit capture recapture (SECR) camera trapping survey was between February and April 2015, thus falling outside the two-year period.

Table 2.1 summarises the methods employed and their associated academic disciplines.

Table 2.1 Summary of methods used in this thesis and their associated academic disciplines.

Method	Discipline area
Semi-structured interviews	Social sciences
Participant observation	Social sciences
Camera trapping	Biological sciences
Questionnaires	Social sciences
Capturing and collaring brown hyaenas	Biological sciences
Scat analysis	Biological sciences

2.3. Ethical considerations

Methods adhered to strict ethical scrutiny throughout the process. I ensured that the rights of humans and brown hyaenas were respected and that this project did not intentionally cause harm to any living beings.

2.3.1. Ethical considerations in social research

The social science research methods received ethical approval from the Department of Anthropology Ethics Committee at Durham University and adhered to the Association of Social Anthropologists of the UK guidelines.

Aldridge and Levine (2001) identify three main areas for ethical consideration when undertaking social research: informed consent, confidentiality, and sensitivity.

Informed consent

All participants gave their informed consent. I visited or phoned community members and landowners to explain the aims of my research and how the data would be utilised in advance. A letter with further information and my contact details was administered to all interested parties. I tried to include people from all sections of the community including women and those who might be marginalised. Participants had regular opportunities to ask questions and all participants understood that they had the right to withdraw from the study at any point. A several weeks grace period after initial contact enabled potential informants to consider my research and decide whether they would like to be involved. At the initial stage I also expressed my intention to share my findings upon the research's completion. I encouraged participants to express benefits they would like to gain from their involvement to ensure that the exchange of information was advantageous for both parties.

I requested verbal or written consent from all people who decided to participate. The written consent form is in Appendix 1. Verbal consent was more appropriate than written consent in the Thalane section of the Buysdorp community, as some informants are illiterate.

Confidentiality

Confidentiality of data was paramount throughout the research process and this was communicated at the onset of interactions to all involved. I anonymised all

participants during analysis. Individuals were assigned a code, which encompassed all information pertaining to their person. If an individual was distinctly identifiable due to uniqueness in his or her circumstances I discussed this issue with the informant and allowed them to withdraw from the study in line with the Association of Social Anthropologists of the UK and Commonwealth Ethical Guidelines for Good Research Practices. I stored physical data in a locked cupboard, which only I had access to, and electronic data was kept in password secure files on my personal computer in line with the Data Protection Act.

Sensitivity

I worked in a community with a very different culture from my own and observed their daily rituals and activities. I tried to ensure that I was unobtrusive and I guaranteed that my presence did not put anyone at risk in any way. I received reports of illegal activities such as poaching protected species. In line with similarly sensitive research scenarios and to protect anonymity (Lewis and Phiri, 1998; Tumisiime *et al.*, 2010), I reassured informants that this information would not be reported to local authorities, as this was not my research goal. I did not want to betray the trust of my informants or jeopardise my objective position. Throughout my fieldwork, I maintained a respectful and professional approach towards local customs.

2.3.2. Ethical considerations in biological research

The biological research received ethical approval from the Durham University Life Sciences Ethical Review Process Committee. The Limpopo Department of Economic Development, Environment, and Tourism (LEDET) granted a research permit to the PPP, which included the capture and collaring of brown hyaenas.

2.4. Study site

The study site is situated in and around the Soutpansberg Mountains, Limpopo Province, South Africa (central coordinates: S23.03788°, E29.44282°). Lajuma

Research Centre in the western end of the Soutpansberg Mountains acted as the base for my research. The privately owned property of Lajuma covers 4.3 km² and is part of the Luvhondo Nature Reserve, which was established in 2011 to protect adjoining private land within the western mountain range for wildlife conservation. In 2011, Dr Russell Hill founded the PPP, which is based at the Lajuma Research Centre. The site also hosts the Durham University Department of Anthropology's undergraduate field course and has served as a field site for several Durham University PhD studies (e.g. Chase Grey, 2011; Coleman, 2013; De-Raad, 2012; Willems, 2007).

The study site covers 5,431 km², which incorporates land situated within the Soutpansberg Mountains and flat-lying areas to the north and the south of the mountain range (Figure 2.1) to facilitate comparisons between montane and low-lying areas and across varying land use types (LUTs). Data were primarily collected on private or communally owned land. Due to the wide-ranging movement patterns of carnivores (Bothma and Bothma, 2012; Gittleman *et al.*, 2001; Kruuk, 2002; Wiesel, 2006) and the mosaic of LUTs they frequent (Kent and Hill, 2013; Thorn *et al.*, 2011b), biological data on brown hyaenas and social data on local people's experiences with hyaenas spans a wide geographical space. This diverse landscape enables exploration into the role of mountains as a refuge for brown hyaenas and other carnivores subjected to human-wildlife conflict.

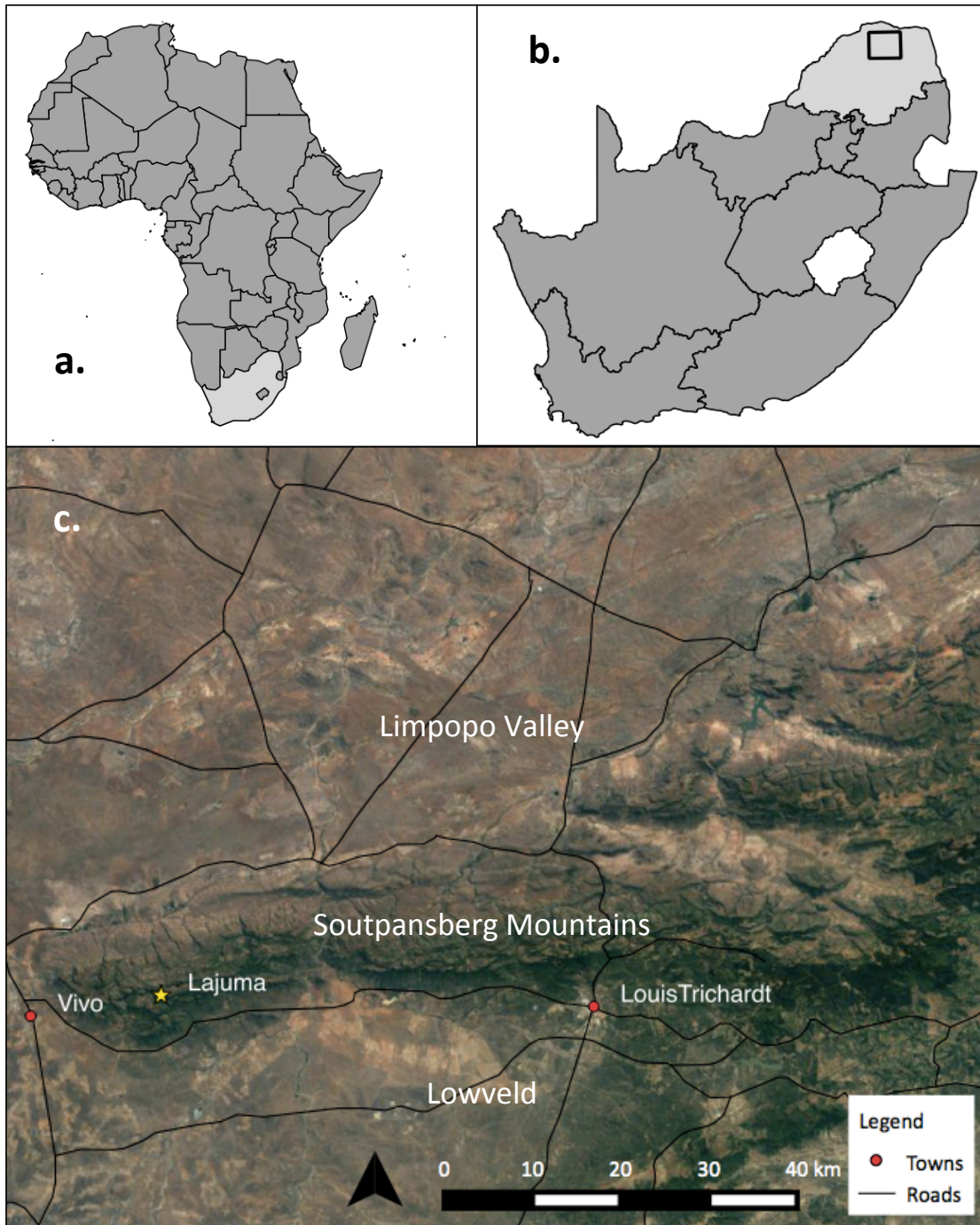


Figure 2.1 Map of the study site. The study site covered 5,431 km² in and around the Soutpansberg Mountains, Limpopo Province, South Africa. a. South Africa's location within the African continent. b. Limpopo Province's location within South Africa with the location of the study site indicated by a rectangle. c. The study site with the Limpopo Valley, the Soutpansberg Mountains, and the lowveld regions labeled. Roads represent tarred roads.

The entirety of the study area is located within the Vhembe Biosphere Reserve, an area that covers 30,701 km² and was proclaimed a biosphere reserve by the United Nations Educational, Scientific, and Cultural Organisation (UNESCO) in 2009 (Vhembe

Biosphere Reserve, 2015). The biosphere reserve stretches from the Soutpansberg Mountains in the south to the Limpopo River in the north and includes parts of Kruger National Park within its eastern boundaries. The area was specifically selected for protection due to its importance for conservation, development, research, and its high level of endemic species (Vhembe Biosphere Reserve, 2015). The Vhembe Biosphere Reserve raises regional awareness and prescribes conservation measures based around sustainable development to government bodies and partner organisations (I. Gaigher, pers. comm.).

2.4.1. Physical geography, geology, and topography

The study area's southernmost boundary is situated 35 km north of the Tropic of Capricorn and the area consists of two distinct biogeographical categories - flat-lying areas and mountainous areas.

Variation in location, climate, biomes, flora, and fauna distinguish between flat-lying areas north of the Soutpansberg Mountains (hereafter referred to as the Limpopo Valley) and south of the mountains (hereafter referred to as the lowveld) (Figure 2.1). Within South Africa the habitat type commonly referred to as the lowveld spans from Swaziland to the Soutpansberg Mountains and the Limpopo Valley includes all land between the Soutpansberg Mountains and the Botswana and Zimbabwe borders (Vhembe Biosphere Reserve, 2008). References to these spaces in this thesis refer to the areas inclusive to my study site unless specified otherwise.

The Limpopo Valley materialised from tectonic activities related to the formation of the Limpopo River shortly after the break up of Gondwana. The area is defined by low undulating plains and scattered kopjes (small sandstone hills) (Vhembe Biosphere Reserve, 2008). The lowveld is characterised by short homogenous scrubland and altitudes generally below 600 m in sea level (Vhembe Biosphere Reserve, 2008).

Separating these two low-lying regions is South Africa's northernmost and least well-known mountain range, the Soutpansberg Mountains (Macdonald *et al.*, 2003). The

Soutpansberg Mountains cover an area of approximately 6,800 km² with altitudes ranging from 200 m above sea level to 1,748 m at its highest point (Berger *et al.*, 2003). The mountain range stretches 210 km from east to west with a north/south width of between 15 km at its narrowest point to 60 km at its widest (Vhembe Biosphere Reserve, 2008).

The Soutpansberg Mountains are composed of quartzite sandstone and basaltic underlying lava built up through volcano-sedimentary succession (Bristow, 1986). The mountains rest along a series of faulted basins which emerged approximately 1,800 million years ago along tension faults (Bristow, 1986). Subsequent volcanic activity produced the first basalt shelf formations (Bristow, 1986). Rock deposits caused by sedimentary succession filled and superseded the basins (Bristow, 1986).

The name, Soutpansberg, is translated from the Afrikaans language as 'Saltpan Mountain'. Naturally occurring salt pans on the northwestern slope supplied communities with salt since prehistoric times (2011). Nowadays, the salt pans produce salt for commercial sale. Many local farmers purchase salt licks for livestock and game animals directly from the pans.

2.4.2. Climate

The Soutpansberg has two distinct seasons - a cool dry winter (May to August) with average temperatures between 12°C and 22°C, and a warm wet summer (December to February) with temperatures between 16°C and 40°C (Kabanda, 2003). September to November and March to April are seasonal transition periods, which experience intermediate temperatures and weather patterns.

Unique climatic conditions in the Soutpansberg Mountains are influenced by precipitation blowing northwards from the Indian Ocean (Berger *et al.*, 2003). As these fronts move upwards, they affect the more southerly lowveld region first. When maritime air and precipitation hits the east-west configuration of the Soutpansberg Mountains, the mountains' undulating valleys, peaks, and contours unevenly disperse

the precipitation resulting in varied climatic conditions within the mountains (Berger *et al.*, 2003). Some montane areas are arid and experience very low rainfall (367 mm per annum) whilst others receive over 2,000 mm of annual precipitation (Kabanda, 2003). The northern and southern slopes of the mountain range are climatically distinct and loosely mimic the climatic variation between the drier, hotter Limpopo Valley and the cooler, wetter lowveld. The arid northern slopes are rockier and more open than the southern slopes where lush mistbelt forests are scattered amongst thick bush (Mostert, 2006).

Northern Limpopo Province, which includes the Limpopo Valley, is characterised by low rainfall and high temperatures. In Messina, South Africa's northernmost town, the average annual high and low temperatures are 29.5°C and 15.4°C. Messina's average annual precipitation is 372 mm (World Climate Guide, 2015). Drought is a regular occurrence in this region and many plants such as baobab trees (*Adansonia digitata*) have adapted to withstand these conditions (Vhembe Biosphere Reserve, 2008). Farming practices have also adapted to the region's challenging climate. In the 1930s at the Mara Research Centre near the Soutpansberg's southern slopes, Professor Jan Bonsma began research to produce a new breed of cattle suitable for the area's sub-tropical climate called the Bonsmara (Swanepoel and Hoogenboezem, 1994). Like the Nguni cattle used by indigenous people for centuries, the Bonsmara is hearty and adaptable in droughts, but the Bonsmara produces a higher carcass weight than the Nguni, making it popular with commercial cattle farmers locally (Muchenje *et al.*, 2008; Venter *et al.*, 1980).

The lowveld has higher rainfall and lower temperatures than the Limpopo Valley due to its position within the catchment area for oceanic weather fronts (Vhembe Biosphere Reserve, 2008).

2.4.3. Flora

The study area, especially the Soutpansberg Mountains, hosts a number of microhabitats and a high level of plant and animal biodiversity resulting from regional

distinctions in climate, geomorphology, and topography (Hahn, 2003a; Macdonald *et al.*, 2003; Mostert *et al.*, 2009).

The two flat-lying areas have more uniform vegetation structures than the Soutpansberg Mountains. The majority of the Limpopo Valley's landscape is covered in Musina Mopane Bushveld and is characterised by dense stands of *Colophospermum mopane* and *Combretum apiculatum* (Vhembe Biosphere Reserve, 2008). The Limpopo Valley acts as a north-south barrier for less xeric species and as an east-west corridor for xeric species (Hahn, 2006). Vegetation is mostly drought resistant and is often influenced by the presence of fire (Vhembe Biosphere Reserve, 2008). Kopjes within the Limpopo Valley support micro-habitats which act as refuges for many plant species and smaller animals (Vhembe Biosphere Reserve, 2008).

The nearby lowveld has a relatively low level of plant diversity. It is primarily composed of Makhado Sweet Bushveld and Tzaneen Sour Bushveld (Vhembe Biosphere Reserve, 2008). The more prevalent Makhado Sweet Bushveld is characterised by short bushveld with an underdeveloped grass layer. Common tree species include *Acacia mellifera*, *Acacia erubescens*, *Acacia tortilis*, *Dichrostachys cinerea*, and *Grewia flava*. Much of the vegetation in this part of the lowveld has been degraded by overgrazing, collection of firewood, and poor fire management (Vhembe Biosphere Reserve, 2008).

The Soutpansberg Mountains support a wide variety of plant species, many of which are endemic (Hahn, 2003a, b; Mostert, 2006). Within southern Africa, no other region has a comparable level of biotope diversity. There are 594 tree taxa and between 2,500 and 3,000 taxa of vascular plants (Hahn, 1997) in the Soutpansberg Mountains (Hahn, 1994). This accounts for approximately one third of all known tree species in southern Africa (Hahn, 1994).

Many local plants have important cultural relevance in traditional medicinal healing (Mathibela *et al.*, 2013; Tshisikhawe, 2003). Even some non-indigenous plants, which are frequently targeted for eradication, have traditional usages by Bapedi healers in Limpopo Province (Semenya *et al.*, 2012).

2.4.4. Fauna

One hundred and fifty-two species of mammals - 62.3% of all South African mammals - occur across the entirety of the Vhembe Biosphere Reserve (based on Friedmann and Daly, 2004). Although no mammal species are endemic to the study site, some species such as the samango monkey (*Cercopithecus albogularis*) are considered vulnerable to extinction (Gaigher and Stuart, 2003; Lawes, 2008).

Biodiversity levels of other taxonomic groups are equally impressive, especially in the Soutpansberg Mountains, where biodiversity is often comparable with or exceeds levels found in Kruger National Park (Foord and Dippenaar-Schoeman, 2003; Gaigher and Stuart, 2003; Gaigher, 2003). Within the Soutpansberg Mountains, 309 species of butterflies, 52 species of dragonflies, 130 species of spiders, 116 species of reptiles, 44 fish species, and 56% of southern African bird species occur (Macdonald *et al.*, 2003).

The prevalence and diversity of predator species varies across the study area. In South Africa, the Limpopo Valley is the last frontier outside of protected areas for many large wild carnivores. Free-roaming lions, cheetahs, leopards, African wild dogs, spotted hyaenas, and brown hyaenas live between the Soutpansberg Mountains and the Limpopo River (Greater Mapungubwe Lion Project, 2015; Lindsey *et al.*, 2004). However, many of these species are facing serious threats from humans. Predators in the study area are killed accidentally and deliberately in snares, road accidents, for body parts used in traditional healing, and because of accusations, real or perceived, of threatening game, livestock, or human wellbeing (Chase Grey, 2011; Collinson, 2013b; Constant, 2014). A small population of approximately 70 lions range between Botswana, Zimbabwe, and South Africa and represent some of the last free-roaming lions in southern Africa (Greater Mapungubwe Lion Project, 2015). This already critically endangered population has sharply declined at a rate of approximately 30% over the past 20 years due to conflict with farmers and prey base depletion (Greater Mapungubwe Lion Project, 2015).

Leopards and brown hyaenas are the primary large carnivores in the lowveld and the Soutpansberg Mountains. A long-term camera trapping survey conducted by the PPP

continually monitors 60 km² of private land at the top of the western Soutpansberg Mountains. Leopards and brown hyaenas are photographed on this camera trapping grid regularly. Spotted hyaenas were recorded six times between July 2011 and January 2015. On all of these occasions photographs featured a solitary individual, suggesting that within the mountains these animals are transitory rather than resident. During the same timeframe on two separate occasions the PPP's camera traps photographed a lone male cheetah and a small pack of African wild dogs.

Leopard population density in the western Soutpansberg Mountains was estimated at 10.7 leopards per 100 km² based on data collected in 2008 (Chase Grey *et al.*, 2013). Subsequent camera trapping data by the PPP indicate a steady and significant decline in leopard density within the same study area between 2012 and 2015 with an estimate of 3.44 per 100 km² at the end of 2015 (Williams *et al.*, in review-b). Despite this decline, leopard numbers in the Soutpansberg Mountains are considerably higher than estimates in the neighbouring lowveld. On commercial farms near the base of the southern and western slopes of the Soutpansberg Mountains leopard density was estimated at 0.7 leopards per 100 km² (Constant, 2014). Conflict with humans, a lower prey base, and less desirable habitats account for discrepancies in density between upland and lowland areas (Gavashelishvili and Lukarevskiy, 2008; Swanepoel *et al.*, 2013).

Small and medium sized carnivores are dispersed across the study area. Species recorded include caracal, serval, African wild cat (*Felis silverstris*), black-backed jackal (*Canis mesomelas*), side-striped jackal (*Canis adustus*), African civet (*Civettictis civetta*), large spotted genet (*Genetta tigrina*), small spotted genet (*Genetta genetta*), aardwolf, honey badger (*Mellivora capensis*), several mongoose species (most commonly banded mongoose - *Mungos mungo*, slender mongoose - *Galerella sanguinea* and dwarf mongoose - *Helogale parvula*), and cape clawless otter (*Aonyx capensis*). These species are evenly spread across low-lying areas, but certain species including aardwolves, jackals, and African wild cats are seldom found in montane areas.

Much of the land in the Limpopo Valley and the lowveld is used for privately owned

game farming or livestock farming. The presence of natural game populations has little impact on livestock production (Dasmann, 1964) and many cattle farmers semi-preserve natural habitats and permit wild game. Consequently, game and livestock farms host large natural prey bases for predators, which includes small antelopes like red duiker (*Cephalophus natalensis*), medium sized antelope such as common duiker (*Sylvicapra grimmia*) and impala (*Aepyceros melampus*), and large ungulates such as greater kudu (*Tragelaphus strepsiceros*) and nyala (*Tragelaphus angasii*). Within the Soutpansberg Mountains, bushbuck (*Tragelaphus scriptus*) is the most common antelope species. A wide diversity of small mammal and rodent species has also been recorded in the area.

2.4.5. Human demography

Limpopo Province in northeast South Africa has a total population of 5,404,868 people who represent a wide diversity of ethnic and linguistic groups (Statistics South Africa, 2012) (Table 2.2 and Table 2.3).

Table 2.2 The percentage of people within ethnic groups in Limpopo Province, South Africa (Statistics South Africa, 2012).

Group	Percentage of people
Black African	96.7
White	2.6
Coloured	0.3
Indian/Asian	0.3
Other	0.2

Table 2.3 Language spoken most often in household per individual household member in Limpopo Province, South Africa (Statistics South Africa, 2012).

Language	Percentage of people
Sepedi	52.9
Xitsonga	17
Tshivenda	16.7
Afrikaans	2.6
Setswana	2
IsiNdebele	2
Other	1.6
Sesotho	1.5
English	1.5
IsiZulu	1.2
SiSwati	0.5
IsiXhosa	0.4
Sign language	0.2

Limpopo Province is one of the poorest provinces in South Africa with many people living in rural areas (Hahn, 2003a) and has the lowest average annual household income in South Africa (Statistics South Africa, 2012).

Although Limpopo Province remains one of the least populous regions in South Africa, Limpopo's population has been steadily rising since the 1996 census (Statistics South Africa, 2012, 2016). Immigration from countries bordering the province to the north contributes towards provincial population pressures. Zimbabwean immigrants seek job opportunities which are no longer available in their home country (Vhembe Biosphere Reserve, 2008). Xenophobia is rife towards the Makwere-Kwere ('strangers' from across the Limpopo River). They are often accused of crime, witchcraft, and stealing jobs and houses from South African nationals (Geschiere, 2009; Hickel, 2014; Landau, 2006) despite the fact that they are infrequently seeking permanent benefits or long-term residency (Landau, 2006).

2.4.5.1. Ethnically descriptive terminology

Personal identity as a concept is defined by a myriad of components including predetermined stable attributes like ethnicity or gender, and changeable and frequently personally selected aspects such as work and interests (Adams *et al.*, 2012; Alberts *et al.*, 2003). Identity can be reflected onto an individual person or a group by applying assumed commonalities (Brewer and Chen, 2007; Oyserman *et al.*, 2002).

From colonial times to present day, one of South Africa's most commonly used categories for considering identity is skin tone (Duncan, 2002). European colonial powers readily categorised people according to their supposed 'race' through hyper-separation. They used these divisions to infer statuses of inferiority and backwardness, often by unjustified exaggeration of characteristics, through assumptions based on the tenets of social Darwinism (Adams and Mulligan, 2003; Dennis, 1995; Plumwood, 2003). These distinctions resulted in inferior treatment and reduction of rights for the 'uncivilised' other (Plumwood, 2003).

In post-apartheid times, many young people are choosing to shed historic prejudices based around 'race'. Modern narratives conveyed by undergraduate students at a historically white Afrikaans university exemplify a more balanced way of understanding identity (Walker, 2005a). Nevertheless, lingering aspects of 'racial' divisions remain (Walker, 2005a). Similar trends are found amongst South African adults and high school students interviewed before and after apartheid (Duncan, 2003). After apartheid, racial discourses in relation to identity reduced in informal conversation (Duncan, 2003). It is worth acknowledging that the campus environment may be more open-minded than other locales within South Africa, especially rural areas.

Although identity in South Africa is beginning to incorporate a broader spectrum of characteristics, 'race', which is more accurately described as ethnicity, is still a key mark of identity. Terms referring to South African ethnic groups are especially salient when defining otherness (Adams *et al.*, 2014). Within ethnic groups, commonalities between religion, regionality, culture, linguistics, and social relations may vary greatly,

so a singular ethnic name is often inaccurately used to classify individuals on the small scale (Adams *et al.*, 2012). However, broader and sometimes extreme cultural and socio-economic differences are connected to previous forms of 'racial' classifications. Three main classifications that echo the apartheid era are commonly and acceptably used within both everyday and formal dialogue in South Africa: black, white, and coloured. The South African government utilises these categories in official reports (e.g. Statistics South Africa, 2012). One of the government's leading approaches to breach the colour barrier in access to employment is entitled 'Black Economic Empowerment (BEE)' (BEESA Group, 2015). On occasion, racist connotations are applied to these terms, however for the most part they have a neutral, non-derogatory, and categorical meaning.

This thesis adheres to categories of black, white, and coloured, not as a means to reinforce discriminatory descriptions, but as a way to discuss important groups and players in line with colloquial and locally acceptable terms. This terminology is applied throughout this thesis to people whom racially and culturally self-identify by these commonly utilised terms.

2.4.6. Ethnic categories in South Africa

Black people compose 79.2% of the population of South Africa and are made up of nine indigenous Bantu-speaking groups (Statistics South Africa, 2012). Historically, black South Africans have been denied or restricted access to education. In 2011, 10.5% of all black South Africans aged 20 years or older lacked any formal schooling (Statistics South Africa, 2012). In recent years, the number of blacks aged between 5 and 24 years attending educational institutions steadily increased (Statistics South Africa, 2016). This is especially pertinent in higher education where black enrolment doubled between 1996 and 2011 (Statistics South Africa, 2012). With the shift towards greater educational access, black South Africans may experience higher average annual incomes in years to come. However, at present this group remains the poorest with the highest levels of unemployment and lowest average annual household incomes (Statistics South Africa, 2012).

White South Africans (8.9%) are of European descent and primarily speak English or Afrikaans (Statistics South Africa, 2012). They are mainly descended from Dutch settlers who migrated to South Africa in the mid-1600s or English settlers who arrived in the early 1800s. In the past 200 years, caucasians from other countries also settled in South Africa (Adams *et al.*, 2014). Nationally, the median equivalised household disposable income for white people is 117,249 South African Rands while the black median income is 10,554 Rands, or only about 9% of the white median income (Gradin, 2014). As a group, white South Africans enjoy the greatest access to education, the highest level of employment, and the highest average annual household income (Statistics South Africa, 2012). These three factors often interlink and create a cycle of perpetuation that secures South Africans of European descent additional benefits such as access to private healthcare and a high level of private land ownership (Cutler and Lleras-Muney, 2006; Walker and Dubb, 2012).

Coloured South Africans comprise 8.9% of the population and are of mixed descent (mostly a mix of Black, Malay, Indian, and European) (Statistics South Africa, 2012). Coloured people most often closely identify with the Afrikaners and share cultural qualities including speaking the Afrikaans language, predominantly subscribing to the religion of the Afrikaners (Protestantism of the Dutch Reformed Church), social practices, and an affinity for certain sports (Farred, 2001). However, coloured people oscillate between the binaries that construct their mixed backgrounds, sometimes preferring traditionally black foods, sports, and cultural experiences (Ebersohn, 2012). Literacy and education levels are improving for coloured South Africans and are higher than the black population's (Statistics South Africa, 2012). Across most socio-economic areas, standards for coloureds rank in between levels experienced by blacks and by whites although these rankings are often closer to blacks' levels (Statistics South Africa, 2012). The majority of coloured South Africans are located in the Western Cape and Northern Cape Provinces (Statistics South Africa, 2012). Limpopo Province has the smallest percentage of coloured South Africans (0.3%) (Statistics South Africa, 2012) and the residents of Buysdorp, a town with approximately 300 coloured inhabitants within my study site, represents one of the most closely-knit and established coloured groups in the region (de Jongh, 2007).

The smallest ethnic group in South Africa are Indians/Asians (2.5%) (Statistics South Africa, 2012) who are descendants of indentured labourers who hailed from the Indian subcontinent in the 1800s (Adams *et al.*, 2014). This group does not feature in this thesis, as they are not prevalent at my study site.

2.4.7. Land use and human impact on the environment

The majority of land in southern Africa can be divided into two distinct spheres - 1) independent freeholds for 'modern' mostly white-owned farming and the commercial sector, 2) the 'traditional' exclusively black farming sector (Murombedzi, 2003). The division between these two land types is marked by the disparity between total land area and government support dedicated to each pursuit (Aliber *et al.*, 2009). Sixty-seven per cent of South Africa's total land area is dedicated to 40,000 mostly white-owned private farms (about 86 million hectares). Only 15% of South Africa's land (about 17.2 million hectares) is black communal land or former homelands. Much of this is state-owned and densely settled (Walker and Dubb, 2012).

Limpopo Province is one of the largest producers of fruit and vegetable products in South Africa (Statistics South Africa, 2010, 2016). The region is also renowned for high levels of game and cattle farming (Statistics South Africa, 2010). In the Vhembe District (a main political district within my study site which includes the Soutpansberg Mountains and land to the south), farming is the second largest economic sector after community services and it contributes to 3% of gross domestic product (The South African LED Network, 2010). Agriculture, predominantly on white-owned farms, employs 22% of the labour force in the Vhembe District Municipality (The South African LED Network, 2010).

White farmers own the majority of the nation's large-scale commercial farms, which produce nearly all marketed output (Aliber and Cousins, 2013). At my study site, the majority of white farmers are Afrikaans-speaking. There is also a number of small-scale, subsistence level farms, which are almost exclusively black-owned and are often managed communally. White commercial farmers interviewed in Limpopo Province

acknowledge the difficulties that black farmers face to be able to enter the commercial farming market due to the large overheads required and a lack of guidance and advice (Genis, 2012). One of the biggest challenges for small-scale farmers in Vhembe District is access to markets (The South African LED Network, 2010).

Large-scale farmers face a number of pressures including production costs, climate, labour issues, uncertainty about government policy, and producer prices (Genis, 2012; Grossman, 1988). In a survey of 141 farmers from Limpopo, Namaqualand, and Overberg, damage-causing animals rated as farmers' ninth greatest pressure (Genis, 2012). Environmental considerations are present in the minds of many large-scale farmers; 50% of respondents experienced pressure to farm more sustainably and 69% of surveyed farmers stated that they have attempted to restore natural resources (Genis, 2012).

In response to environmental and financial challenges, many cattle farms across South Africa have converted to game farming (van der Merwe and Saayman, 2005). The area north of the Soutpansberg Mountains was once largely devoted to cattle farming, however in 2003 it was estimated that 80% of the former cattle ranches had transitioned to game farming (Macdonald *et al.*, 2003). Game ranching is a growing industry due to the lucrative commercial value of game through ecotourism, hunting, breeding rare game species, and venison sales (van der Merwe and Saayman, 2003; van der Waal and Dekker, 2000). Trophy hunting and biltong hunting⁴ generate the largest income of all private game farm activities (van der Merwe and Saayman, 2003) and are extensions of colonial ideals of 'taming' nature and domination over large dangerous wildlife (Goodrich, 2013). Throughout colonial times and to an extent today, large game animals are considered the property of a racial and class elite, namely white hunters or tourists (Adams, 2003). Fences, high costs of hunting or tourism, and the illusion of untouched wilderness for whites only regenerates the practice of excluding certain social groups from interacting with nature (Adams and Mulligan, 2003).

⁴ Hunting for meat or animal body parts for utilisation is referred to as biltong hunting.

The transition towards game farming has had mixed conservation outcomes. By placing a monetary value on wild animals, wildlife numbers in South Africa are higher than they have been for many years (Carruthers, 2008). Private game farming in Limpopo Province is estimated to host greater game species' densities than Kruger National Park for all species except Burchell's zebra (*Equus burchelli*) (van der Waal and Dekker, 2000). Hunting areas often have 'vulture restaurants', places where carcasses are disposed of. These areas have a positive impact on local predator abundance but also bring negative effects such as possibly increasing the spread of rabies and disrupting natural feeding systems; this is especially relevant for scavengers such as brown hyaenas and jackals (Yarnell *et al.*, 2014).

Across the study site, land bought as weekend or holiday retreats for city-dwellers primarily based in Gauteng Province or abroad has increased. These properties are often kept naturally pristine and have minimal human impact (Vhembe Biosphere Reserve, 2008).

Despite current land use management producing some positive conservation outputs, natural habitats and wildlife are facing threats locally from the development of forestry plantations, urban sprawl, human population pressure, agricultural expansion, mining, and overgrazing (Vhembe Biosphere Reserve, 2008). Poverty, low education levels, and unemployment are typical in Limpopo Province and lead to illegal natural resource extraction and wildlife practices such as snaring and poaching. *Bushmeat* (section 1.3.3) hunting is connected to poverty and low protein intake (Nielsen, 2006). Wire snaring is often concentrated near roads, crops, human settlements, or permanent water sources (Watson *et al.*, 2013).

2.5. A postcolonial approach

An interdisciplinary approach combining social and biological methods is integral to my examination of relationships between humans and brown hyaenas. Equally integral is a postcolonial contextual discourse. European expansion across South Africa in the 1800s and associated politics and policies define the contemporary human and

environmental landscape in northern Limpopo Province. Although the 'Rainbow Nation' of South Africa is no longer under colonial rule, colonialism and its ideological companion, apartheid, have made a lasting mark on South Africans' beliefs and relationships with nature today (Erasmus and Pietrse, 1999; Steyn, 2005). Apartheid and imperialist racial divisions still haunt South Africa. Young black people are at a disadvantage in the quest for academic success and employment (Bauer, 2012). Exclusionary policies over access to nature which were created in colonial times affect modern black South Africans' perceptions about visiting national parks (Butler and Richardson, 2015). This concept is captured by Lowenthal (1997, p. 232) – "We inherit colonial habits along with degraded habitats".

Sharp (2009, p. 3) argues that the concept of postcolonialism has two different interpretations depending upon punctuation. The hyphenated post-colonialism examines geographical areas and historical periods following the end of colonisation. Postcolonialism as a compound word, explores how people and places are continually affected by colonial power structures beyond the official end of colonisation (Sharp, 2009, p. 4).

In this thesis, a postcolonial approach is applied to understand how the legacy of European dominance in the area shaped modern power structures, access to resources, and attitudes towards dominance over nature. These findings will be related to the status of and future conservation agenda for vulnerable predators such as brown hyaenas. Generally, postcolonialism has negative connotations (Sharp, 2009), however this thesis aims to determine whether the postcolonial landscape has affected human connections with hyaenas positively as well as negatively.

2.6. Historical context

An introduction to the national and regional history with an emphasis on colonial and postcolonial developments is necessary to contextualise this thesis and its themes. Human-induced environmental changes are highlighted throughout this brief history.

2.6.1. Precolonial history (around 28,000 B.C. – 1652)

The San people were the first indigenous southern Africans. These nomadic hunter-gatherers followed mobile herds of prey to hunt meat sustainably for at least 30,000 years (Beinart and Coates, 1995). In anthropology, the concept of the ‘noble savage’ living in harmony with animals and with nature is common, although it is increasingly questioned (Booth, 2003; Elder *et al.*, 1998; Ellen, 1986; Kallard, 2003). Like the Native American tribes, this group acquired a reputation for living in balance with nature (Beinart and Coates, 1995; Ellen, 1986). The San utilised every aspect of an animal carcass (Beinart and Coates, 1995). Although their status as harmonious with nature is largely justified, their presence affected the landscape. They burnt large areas to invite fresh grass growth and lure prey. In the nineteenth-century, the San were observed driving herds of game into pitfalls in numbers too numerous to consume (Beinart and Coates, 1995).

The San first penetrated the central Limpopo basin around 5,000 years ago and were followed by the Khoekhoen, nomadic pastoralists who arrived in South Africa around 2,000 years ago (Eastwood and Eastwood, 2006). Early agrarian societies of Bantu origin migrated southwards from Nigeria and the Congo settling along the Limpopo River around A.D. 300 (Thompson, 2001). Distinctly styled rock art paintings by the San, Khoekhoen, and Bantu-speaking agro-pastoralists (Northern Sotho) occur within the Soutpansberg Mountains and the wider Limpopo Valley (Eastwood and Eastwood, 2006; Eastwood, 2003).

The Iron Age kingdom of Mapungubwe, which incorporated an area spanning from the Soutpansberg Mountains in the south to Zimbabwe’s Matopos region in the north, came to power in A.D. 800 (Wolf, 2011). The city of Mapungubwe near the Limpopo River was an important trading post between southern Africa and the Orient. Foreign trade led to Mapungubwe’s rise and eventual fall in A.D. 1150 (Eastwood and Eastwood, 2006).

2.6.2. European settlement and colonisation (1652 – 1948)

Portuguese explorer, Bartholomeu Dias, was the first European to reach South Africa when he docked at Mossel Bay in 1487 (Crosby, 2004; Thompson, 2001). The Dutch East India Company established the first permanent European settlement in South Africa in 1652 (Thompson, 2001). Between 1652 and 1795 Dutch settlers redefined themselves as Afrikaners, also known as 'Boers', and laid the foundation for colonisation in South Africa through territorial expansion, conquering indigenous people, and importing slaves (Thompson, 2001). The British permanently settled in the Cape Colony in 1820. Their presence and new legislation prompted the exodus of 5,000 Afrikaners from the Cape. In the 1830s and 1840s this group, later referred to as voortrekkers, embarked on journeys to colonise new tracts of land under Dutch rule (Carruthers, 2008). The voortrekkers forged areas to the north and the east of the Cape Colony during 'the Great Trek'. Tensions between the Afrikaners and the British persisted and eventually came to a head during the second Anglo-Boer War (1899 – 1902). Britain was the victor and in 1906 and 1907 the Afrikaans former republics were allocated parliamentary governments. In 1910 the British-ruled Union of South Africa was formed joining the Cape Colony, Natal, the Transvaal, and the Orange Free State (Thompson, 2001).

Following the conquest of the Venda, the final independent native group in southern Africa, authoritarian rule over the black population was cemented with the beginning of segregation laws (Thompson, 2001). The right to own or rent land became dependent upon racial classifications with the Native Lands Acts of 1913 and 1936 (Magome and Murombedzi, 2003). Blacks were only allowed ownership of 13% of the country's land area (Magome and Murombedzi, 2003). After 1914, almost the entire black population was living 'illegally' in white areas (Hay, 2014). With limited remaining land rights, black South Africans were evicted to 'native reserves', later known as 'homelands', based on cultural and linguistic allegiances (Magome and Murombedzi, 2003). By design, these areas were often infertile or agriculturally unproductive which forced many black males to work as migrant labourers in gold mines or on maize farms (Magome and Murombedzi, 2003).

The Union of South Africa's vast size combined with the geographical separation from the ruling Cape Colony made jurisdiction challenging. Colonial powers relied upon white subjects to police the black population and assert control over the landscape (Milton, 1997).

2.6.2.1. Colonisation across the study site

The European advance brought great changes to the study area's social and cultural composition including the introduction of the Afrikaans language, Calvinism, Roman-Dutch law, and European-influenced social and economic practices (Vhembe Biosphere Reserve, 2008).

The first European colonist to arrive in northern Limpopo was Coenraad de Buys in 1820. His arrival preceded the Great Trek colonists who are commonly viewed as the first Europeans in Limpopo. De Buys fled the Eastern Cape where he was branded an outcast and criminal (de Jongh, 2006). He cohabitated with several local women and fathered nine known children (de Jongh, 2006). After reaching an agreement with the resident Venda chief, Ramavhoya, De Buys' family settled in the western Soutpansberg Mountains at a place originally called Mara (Figure 2.2). De Buys' second born son, Michael, became the first acknowledged leader of the Buys community at their contemporary location (de Jongh, 2006). In his later years, following the death of his wife, Elizabeth, De Buys journeyed to Mozambique and, unexpectedly, never returned (de Jongh, 2006).

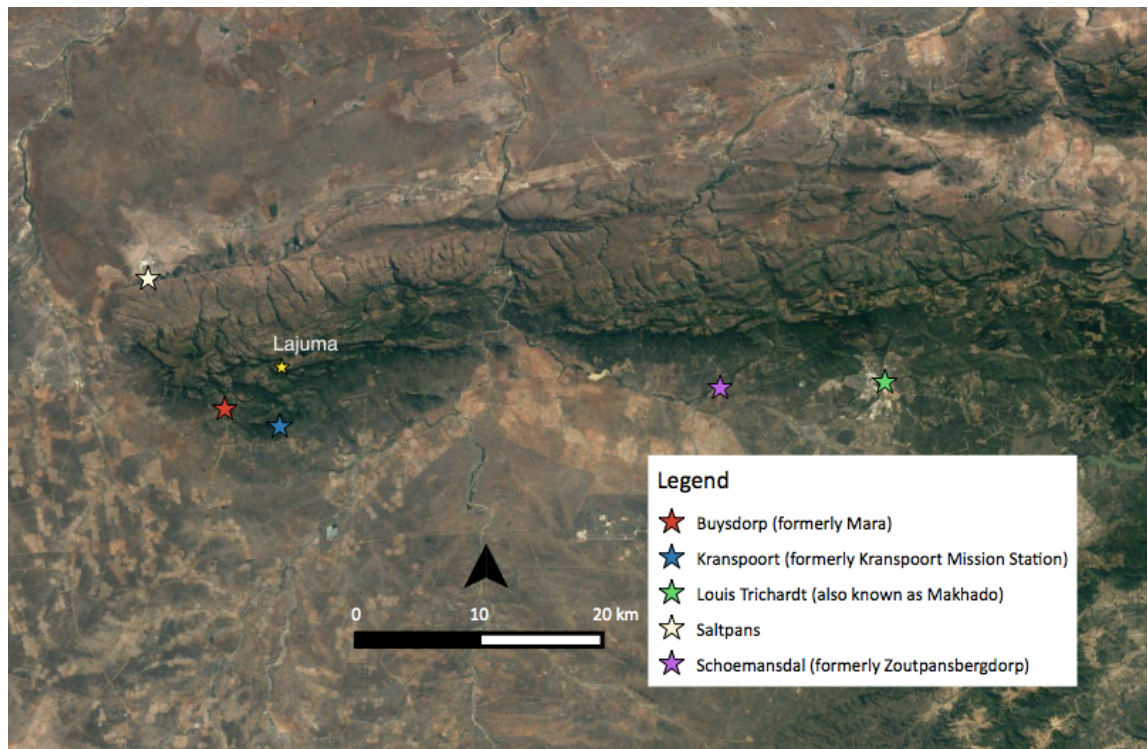


Figure 2.2 Map of the Soutpansberg Mountains, South Africa, showing colonial settlements in relation to Lajuma's location.

In Coenraad de Buys' lifetime the mostly coloured members of the Mara community adopted customs associated with black Africans such as polygyny, but these practices were banned by Michael following his father's death. This initial push towards preserving their European roots, practices, and the Dutch language led to de Buys' descendants (the Buys) regarding themselves as superior to the local population (de Jongh, 2004). This Eurocentric position may have been influenced by governmental changes which restricted civic rights to coloured and black people (de Jongh, 2006). The Buys were exempt from some exclusionary regulations. They maintained the right to carry guns due to services rendered to the state by supporting the voortrekkers and 'Boers' in skirmishes with the Venda and other local people (de Jongh, 2004). In 1871 many of these allocated rights were removed when the Buys were classified as 'natives' following the British annexation. President Paul Kruger allocated 11,000 hectares of land to the Buys people in 1888 as a token of appreciation for their services to the Transvaal Republic (de Jongh, 2006). Today Mara is renamed Buysdorp and members of the community still cling to their European roots and revere the community's founding father, Coenraad de Buys (de Jongh, 2004).

The voortrekkers arrived in the area several years after De Buys. Louis Trigardt, the leader of the first voortrekker party to reach northern Limpopo, arrived in the Soutpansberg region in May 1836, first settling near the saltpans on the north side of the mountain (Figure 2.2) but moving to the southeastern side later on to escape the heat and pestilence (Wolf, 2011). Trigardt died in 1837 of malaria on a journey to Mozambique but he left a long-lasting legacy to the region. Colonists followed in his footsteps and established permanent settlements in the area (Wolf, 2011). Louis Trigardt is the namesake for one of the largest towns in northern Limpopo Province (Figure 2.2). Nowadays, the town's name legally changes on an almost annual basis between the names 'Louis Trichardt' and 'Makhado'. Makhado was a prominent Venda chief in the 1800s that fought against the voortrekkers. The town's continual renaming, which has been accompanied by the removal and erection of commemorative statues of these two historical namesakes, reflects local ethnic groups' conflicting ambitions to venerate either the area's Venda or Afrikaans histories (Thotse, 2010).

In May 1848 near to the area Trigardt stayed, voortrekkers led by Andries Hendrik Potgeiter established the settlement of Zoutpansbergdorp (Figure 2.2), later named Schoemansdal following Potgeiter's death. Schoemansdal had a short history due to conflict with the local Venda chiefs, and Makhado in particular. The town was burnt and evacuated during a Venda raid in 1867. Other factors contributed to the demise of Schoemansdal including habitat degradation (Wolf, 2011). However, during Schoemansdal's reign more white settlers arrived and began to farm independently.

Mission stations developed in the Soutpansberg area in the late 1860s. Blacks who worked as migrant labourers in Natal and the Cape Colony in the 1860s had already introduced Christianity to the region to some extent, although the response to this new religion was mixed (Kirkaldy and Kriel, 2003). In order to convert local people to their religion, missionaries took meticulous care to learn about all aspects of native life and record these detailed but potentially biased observations in writing and photographs (Kirkaldy and Kriel, 2003). The missionaries introduced the first Western education and hospital services to the indigenous people (Kirkaldy and Kriel, 2003). Kranspoort is the closest colonial mission station to Lajuma (Figure 2.2). In the 1950s,

it ceased to function as a mission station (Malunga, 1986) and nowadays, it is a small rural community.

2.6.2.2. Colonisation and the environment

The arrival of white colonists in the area was shocking for many indigenous inhabitants. Nancy Mathews' memoir about growing up on the slopes of the Soutpansberg Mountains in the 1920s and 1930s expresses this sentiment: "Andries lived in one of the huts on the farm with...his very old mother...She remembered seeing the first white man who ventured into the remote area of the Transvaal where they were living at the time. As nobody in their village had ever seen a white man before, she and her brothers and sisters all ran, screaming and terrified, back to their home to tell their family about the 'ghost' they had seen walking about the veld killing animals." (Mathews and Smith, 2006, p. 61)

Colonisation enables full appropriation of exportable resources by inflicting political control over land and indigenous people. Colonial conquests in Africa were primarily designed to cheaply produce large quantities of resources (Crosby, 2004; Lowenthal, 1997). This process often led to an ideological and physical subduing of the wilderness and its inhabitants with the intention to civilise both (Lowenthal, 1997).

Colonial powers believed that they had a duty to 'tame' the wildness of the lands they occupied through imperialism, land management, hunting, and collecting zoological specimens (Adams and McShane, 1996; Adams and Mulligan, 2003; Ryan, 2000). The wildness of Africa, which was romanticised and homogenised, was symbolic of the uncultured and uncivilised landscape and people living there (Adams and McShane, 1996; Adams, 2003; Adams and Mulligan, 2003).

Through the process of 'taming' the wild and extracting resources, European settlers in the 1800s substantially altered northern Limpopo's environment to an extent and level of permanency which drastically exceeded the impact of indigenous activities (Vhembe Biosphere Reserve, 2015). Prior to European exploitation in the area's early

colonial period, ancient forests of sneezewood (*Ptaeroxylon obliquum*) and Outeniqua yellowwood (*Afrocarpus falcatus*) dominated the landscape around the Soutpansberg Mountains. These enormous trees, which produced wooden planks up to 27 m in length, were removed in their near entirety for colonial export (Vhembe Biosphere Reserve, 2008). Early colonial settlers were responsible for mass declines in numbers of native animals. The arrival of firearms and advanced traps, and pressure to supply a growing international market with animal parts accelerated the rate at which hunting in Africa was conducted (Adams, 2003). Ivory, timber, hides, and potentially rhinoceros (*Ceratotherium simum* and *Diceros bicornis*) horn was traded on large-scale between Schoemansdal and traders from the east coast and the Cape Colony. African elephants (*Loxodonta africana*), which are now locally extinct in the southern Soutpansberg, were once common in the area surrounding Schoemansdal. During the settlement's 19-year history, an estimated 90,900 kg of ivory was exported from Schoemansdal to Mozambique, Natal, and the Cape Colony (Wolf, 2011).

The arrival of guns also influenced indigenous people's relationships with the environment (Beinart, 1989). The Venda people first acquired firearms from settlers in Schoemansdal who commissioned them as hunters. After Schoemansdal's demise, the Venda people under Makhado's leadership continued the tradition of mass hunting with firearms (Wagner, 1980).

Sport hunting was a popular pastime, especially amongst British colonists who viewed the indigenous African and Boer practice of hunting for skins as backwards (Beinart, 1989; Carruthers, 2008). Animals that posed a potential threat to farming such as large cats, hyaenas, and jackals were killed as vermin (Beinart, 1989; van Sittert, 2005). Authorities offered financial rewards for predator pelts in the early 1900s to improve settler stock farming (Beinart, 1989).

The first concerns about the survival of large game animals such as elephant, rhinoceros, and hippopotamus (*Hippopotamus amphibius*) arose at the end of the nineteenth-century after decades of mass commercial exploitation of local species (Vhembe Biosphere Reserve, 2008). Colonial administrations formally acknowledged Africa's dwindling wildlife numbers as early as 1900 when authorities met to sign a

convention for the preservation of African animals, birds, and fish. However, this convention was never actively implemented (MacCormick, 1989).

The establishment of Kruger National Park in 1926 was in response to the overhunting of megafauna (Carruthers, 1997). The movement to establish national parks spread globally from the United States in the first half of the twentieth-century as a means to preserve the 'chaos' of nature and bestow the 'order' of man (Carruthers, 1997). National parks adopt a fortress approach to conservation, creating exclusionary areas which are preserved for the people but also protect them from the people; creating a landscape of conservation winners and losers (Binnema and Niemi, 2006; Robson and Berkes, 2010). Prior to receiving its protected status, Kruger National Park was home to black residents. Their presence 'spoiled' the western illusion of wilderness and preservationism as being devoid of humans or human impact (Adams and McShane, 1996; Beinart, 1989; Berglund and Anderson, 2003; Neumann, 1998). In an attempt to deculture and 'naturalise' the landscape, authorities either removed or hid black residents from the public eye (Beinart, 1989; Magome and Murombedzi, 2003).

Regardless of the staggering numbers of trophies and ecological specimens collected during the 1800s, hunters and colonial administrations averted responsibility for the decline in African fauna by placing blame on black African hunting practices and branding black hunters as poachers and criminals (Adams and McShane, 1996). Portrayals of the European hunter, on the other hand, depicted an adventurous hero who was exalted by European society (Ryan, 2000). Colonists were quick to ascribe characteristics of the African living in primitive harmony with nature or as an ignorant and dangerous destructor of nature as it suited (Adams, 2003; Carruthers, 1997). In response to large game losses, blacks were banned from hunting, even if done sustainably with low impact weaponry on land they had utilised for centuries. This was achieved through gun and game laws, and denial of access to game-rich patches of land through the creation of game reserves and the implementation of land laws (Adams and McShane, 1996; Adams, 2003; Carruthers, 1997; Ryan, 2000). White participation in hunting continued and even accelerated in some cases under auspices of sample collection for scientific enlightenment and conservation (Adams and McShane, 1996).

In the nineteenth-century new concepts and ideas about the natural environment developed in European culture. The environment was defined as the part of nature that impacts humans but this definition stipulated that people were most assuredly not part of the environment despite their proximity (Kesby, 2003). “Concepts of nature are always cultural statements” (Beinart and Coates, 1995, p. 3) and they are fluid, difficult to understand, and to deconstruct (Gombay, 2014). Shifting definitions of poaching and nature, for example, depend on viewpoints within the colonial and postcolonial contexts (Gombay, 2014). Poaching is associated with trespassing and the violation of ownership rights, but in South Africa where land was continually taken and given back, even understanding who legitimately owns the land is challenging (Gombay, 2014).

2.6.3. Apartheid (1948 – 1994)

Following the 1948 general election, the Afrikaner National Party gained power (Thompson, 2001). This party remained in office until 1994 and formalised discriminatory policies against non-whites under apartheid. The Population Registration Act of 1950 classified all South Africans by race. The 1950 Group Areas Act forced racially similar groups to cohabit in racially zoned areas (Thompson, 2001).

The Groups Areas Act and the Native Resettlement Act amalgamated small independent cultural groups into overarching tribal homelands. Homelands intended to unite analogous tribal groups but in reality similarities were often imagined and idealistic. These regulations provoked cultural disintegration and replacement of locally specific cultural customs within rural communities (Hay, 2014). Between 1960 and 1980 approximately 3.5 million people were removed and placed in occupied homelands (Wels, 2003). The homeland designated for the Venda people of northern Limpopo incorporated their capital, Thohoyandou, and covered 6,500 km² (Wolf, 2011). Despite losing many rights during apartheid, coloured people were not transferred to a homeland as they lacked common ancestral rights to a geographic zone (Erasmus and Pietrse, 1999).

Under apartheid, racial divisions cut across all aspects of society including access to public services, equal wages, and the job market. Racial mixing was discouraged through geographical separation, emphasising linguistic and cultural differences, and perpetuating a boss/servant hierarchy (Thompson, 2001).

In 1961 South Africa became an independent republic separate from the British Commonwealth (Thompson, 2001). Many African countries received colonial independence around this time, which led to a continent-wide surge in desegregation and democratic practices. In contrast, South Africa's strong apartheid policy remained intact, attracting attention on the international stage as an example of a semi-industrialised country reinforcing inhumane and archaic practices (Thompson, 2001). International resistance to the apartheid formulated late due to fears of creating a political enemy with access to valuable economic resources and the potential to become an anti-communist ally (Thompson, 2001). In 1977 the United Nations Security Council placed an embargo on dealing arms to South Africa. This coincided with the fortification of civil rights and anti-racist opinions in American politics (Thompson, 2001).

Opposition was also rife within South Africa with regular uprisings from the African National Congress (ANC) and the Pan-Africanist Congress (PAC) as well as independent groups. Many of these rebellions ended violently despite initial attempts at peaceful demonstrations. The Afrikaner National Party responded to these revokes with violence and sentenced ANC and PAC leaders including Nelson Mandela to life imprisonment in 1964 (Thompson, 2001).

By the mid 1980s South Africa encountered regular domestic uprisings and mounting international pressure. The government proclaimed a national state of emergency in 1986 and under the leadership of Frederik Willem de Klerk, began to reform and eventually withdraw apartheid regulations. Profound changes occurred in the early 1990s with the reinstatement of banned opposition parties, the release of Nelson Mandela and other political prisoners, and the revocation of many land acts restricting black movement (Thompson, 2001). Apartheid ended on April 27, 1994 with the

election of the ANC in the country's first democratic and multiracial election (Thompson, 2001).

2.6.4. Post-apartheid (1994 – present day)

With the dissipation of apartheid, South Africans had to reconsider their ethnic identity. This was especially relevant for the Afrikaans-speaking cohort who shifted from a position of political power to a more vulnerable minority status (Korf and Malan, 2002). Despite the abolition of strict apartheid laws, racial segregation remained informally through social, political, and economic differences (Glaser, 2010)

The post-apartheid democratic governments pledged to readjust the racially divided balance of power and wealth by improving benefits for black South Africans, mainly through initiatives such as BEE, fast-tracking development, and land redistribution (Aliber and Cousins, 2013; Glaser, 2010; Magome and Murombedzi, 2003). These programmes have attained limited success thus far. BEE has also attracted criticism and been branded as racist against whites. Some young white males feel like BEE excludes them from opportunities within the job market based on their physical characteristics (Fraser, 2008).

In South Africa, land redistribution is centred around the Restitution of Land Rights Act 22 of 1994 which aims to restore land to people who lost land rights due to racial laws implemented after June 19, 1913 (Magome and Murombedzi, 2003). Through restitution, redistribution, and tenure reform the government aims to improve livelihoods for people who can not afford to purchase land (Magome and Murombedzi, 2003). The land restitution process in South Africa is centred around a willing seller - willing buyer scenario whereby the government must offer market incentives to interested sellers (Fraser, 2008). However, many landowners refuse to sell because they are personally attached to their land, have materialistic or symbolic investments in the land, or they fear the risks of re-establishing themselves elsewhere (Fraser, 2008; Fraser, 2012). The process for claiming land is challenging. Claims are processed through land claims courts, an expensive and lengthy procedure which has

deterred many potential claimants (Magome and Murombedzi, 2003). The government stated its aim to redistribute 30% of total agricultural land by 2014 (Fraser, 2006), but only about 7.5% had been reallocated by 2012 (Nkwinti, 2012).

Unfortunately, since 1994 some socio-economic conditions have worsened for South Africans, especially the black majority (Magome and Murombedzi, 2003; Oosthuizen and Bhorat, 2004). In Limpopo Province, unemployment rose from 42.2% in 1995 to 56.5 % in 2002 with rural areas such as my study site affected significantly worse than urban areas (Oosthuizen and Bhorat, 2004). Limpopo Province had the greatest surge nationwide in discouraged work-seekers, individuals who have given up on actively seeking work, from 12.7% in 1995 to 21.2% in 2002 (Oosthuizen and Bhorat, 2004). Poverty incidence increased in Limpopo Province from 65% of the population in 1995 to approximately 75% in 2000; this represents the most dramatic increase nationally (Özler, 2007). The risk of poverty in Limpopo Province almost exclusively affects black people and the incidence of poverty is virtually zero for white people (Özler, 2007). Poor economic security and extreme disparities between ethnic groups can contribute towards human-human factors behind human-wildlife conflict (Rust *et al.*, 2016).

Chapter 3: Attitudes, experiences, and perceptions of brown hyaenas

3.1. Introduction

Thinking with animals incites self-reflection on humanity, hence the popularity of animal imagery in marketing campaigns, stories, and as symbols (Arluke and Sanders, 1996; Daston and Mitman, 2009; Knight, 2005; Mullin, 1999). Social constructions commonly define relationships with non-domesticated animals as direct involvement lessens (Gullo *et al.*, 1998). Ideas about animals often develop from personal opinions extended out to a wider audience with limited knowledge or experience of the animal (Gullo *et al.*, 1998). As a result, perceptions of animals or practices involving animals do not always align with biological realities, creating challenges at the interface between species conservation and cultural practices. For example, even though countries like the UK and the US no longer hunt whales for meat or oil and many people have no experience with whales in real life, members of the public construct mental relationships with these animals largely in accordance with the media's influence (Einarsson, 1993; Milton, 2005). The ethnocentric practice of attributing symbolic and anthropomorphic qualities to whales made them metaphorically 'good to think' for many people outside of the whaling industry (Einarsson, 1993). This process created an affinity and sympathy for whales and increased public and political pressure to disband whaling (Einarsson, 1993). With the reduction in whaling, Scandinavian and Japanese fishermen lost their livelihoods, homes, and heritage, and were villainised despite their fishing practices being extremely low impact (Einarsson, 1993). Small-scale subsistence hunting of whales by Inuit communities has also been banned, causing severe impacts on cultural practices and natural resource availability for an indigenous group (Langton, 2003).

Animals are often classified into categories of 'good animals' and 'bad animals' through societal depiction (Cassidy, 2012; Sax, 2007). Species considered oddities that fail to fit into a clear category are often ignored, segregated, loathed, or destroyed by humans (Arluke and Sanders, 1996). Equally despised are 'dirty' animals such as rats

and mice, which are not contained in their prescribed place and can cross into human geographies (Arluke and Sanders, 1996; Douglas, 1966). Towards the bottom of the socio-zoological ranking are predators - animals which pose a threat to human wellbeing through domestic animal predation or man-eating (Arluke and Sanders, 1996, p. 175). These creatures are frequently demonised because they break the normative order of human domination over animals (Hurn, 2012, p. 78). They are considered to lack fear of humans and imbue trepidation in people instead (Arluke and Sanders, 1996; Kruuk, 2002). Predators that are guilty or perceived to be guilty of human-wildlife conflict are alleged to be the worst of the 'bad animals' due to geographical encroachment, indiscriminate killings, and, in cases such as the brown hyaena, failure to ascribe to a clear category.

The way in which societies portray animals, and especially carnivores, moulds attitudes and influences actions towards them (Brownlow, 2000; Jones, 2011; Woods, 2000), thus emphasising the importance of understanding how humans relate to predators in conservation. This chapter aims to investigate how different socio-cultural groups situated in and around the Soutpansberg Mountains experience brown hyaenas, both through actual interactions and mental constructions of the species.

3.2. Perceptions of hyaenas

Brown hyaenas are more secretive than many other African predators (Mills, 1990; Mills and Hofer, 1998). They forage solitarily, are seldom vocal, and walk at night (Mills, 1990; Stuart and Stuart, 2007). As a result, they can live in close proximity to humans for long periods before being detected (Kuhn, 2014). Many people living in areas where brown hyaenas are present will never see one and therefore the animal exists almost exclusively in their minds. With the advent of modern technology, a person living in Europe or America may have more intellectual access to brown hyaenas through the internet and wildlife documentaries than someone living in southern Africa (Milton, 2002). This illustrates the importance and variability of visibility and invisibility in understanding animals (Burt, 2001).

Animals are used in some sub-Saharan African storytelling and folklore. Culturally, species are symbolically grouped into physical levels – sky, middle level, below, and waters (Kesby, 2003; Morris, 1998). The middle level is the arena in which human activity occurs and large felids are often key animals found in stories based at this level (Kesby, 2003). Although traditionally some sub-Saharan African languages do not have a word equivalent to mammal, many languages have a descriptive word for ‘animals like us’, which encompasses middle level species (Kesby, 2003). Also within the middle level are species that are set apart from humans because they are considered malicious, sinister, or bold, and therefore linked with witches (Kesby, 2003). Hyaenas, and especially spotted hyaenas, fall within this category. Although they are recognised as being an ‘animal like us’, they sit on the edge of this category and are feared and hated (Kesby, 2003). This feeling of negativity towards hyaenas is summed up by Kruuk (1975; p. 49), “To natives and visitors of Africa alike, no creatures are more loathsome than 'fisi'.” (fisi is Swahili for hyaena).

In stories, animals are often described as if they possess human characteristics (Daston and Mitman, 2009). Many traditional stories from Malawi are situated in villages and describe animals speaking and conducting human activities (Morris, 1998). Although a wide variety of species are mentioned in Malawian folktales and proverbs, the six most commonly discussed animals are the leopard, the lion, the hyaena, the hare, the elephant, and the tortoise (Morris, 1998). Within sub-Saharan African stories a common theme is that of the ‘Trickster’, a small animal such as a hare, tortoise, spider, or jackal who tries to fool his opponents but is sometimes outwitted himself (Kesby, 2003). The cunning ‘Trickster’ will commonly target larger mammals in his deceptions and hyaenas frequently fulfil this role in mythology and storytelling (Kesby, 2003). The hyaena is often depicted as a foolish, easily tricked coward (Glickman, 1995; Kruuk, 1975, 2002).

There is often a discrepancy between the hyaena depicted in folktales and the hyaena in real life. For example, the Himba people of north western Namibia tell stories which portray the hyaena as stupid and weak (Crandall, 2002; Weingartner); however, they maintain that the hyaena is a deadly and dangerous killer of livestock (Crandall, 2002).

Amongst mammals, hyaenas have one of the worst reputations. Their negative status spans cultures, geography, and history (Glickman, 1995). Although an overall disdain for hyaenas is present in African and Euro-American culture, in the west they are more prominently seen as ugly and cowardly, whereas in Africa their defining characteristics are greed, gluttony, stupidity, and foolishness (Crandall, 2002; Frembgen, 1998; Glickman, 1995; Kruuk, 2002). However, the African perception is often countered with an appreciation of the hyaena's power and dangerous nature (Glickman, 1995). The public image of hyaenas is largely based on traits existent in the spotted hyaena but transcends the species barrier and is liberally applied to the other species in the Hyaenidae family (Glickman, 1995; Mills and Hofer, 1998). Negative imagery of hyaenas is found in modern western media such as the 1995 Disney film, *The Lion King*, and literature such as Ernest Hemingway's novel, *The Green Hills of Africa*, but the origins of these perceptions can be traced as far back as 2,300 years in Aristotle's *History of Animals* (Glickman, 1995).

Negative perceptions towards hyaenas also generated from associations with necrophagia (Kruuk, 2002). Many cemeteries in east Africa have high walls surrounding the perimeter to keep hyaenas out (Gade, 2006). In the Middle Ages, animals were frequently used to convey moral messages or to propagate religious beliefs in bestiaries or 'books of beasts' (Kalof, 2007). Hyaenas featured in bestiaries predominantly as monstrous biologically inaccurate grave robbers eating the dead or as promiscuous creatures, which have the capability to change sex (Glickman, 1995; Kalof, 2007). The hyaena was used in bestiaries as a symbol of impure and sinful behaviour while animals like the elephant, which were believed to only mate once in a lifetime, were portrayed as virtuous (Kalof, 2007). The hyaena is also negatively construed because it scavenges, which means it does not fall within a clear category of a predator or a prey species (Wilson, 2003). Scavengers such as vultures also have negative connotations due to their links with death and the macabre despite the fact that scavenging is an important ecosystem function which reduces disease transmission and contamination from carrion (van Dooren, 2010).

Depicting animals like the hyaena as 'bad' can affect how people respond to the species (e.g. Boissonneault, 2011; Einarsson, 1993; Peace, 2002). In other words

“perception itself is a value-realizing, value-organizing activity” (Caporael and Heyes, 1997, p. 69) and perceptions either endanger or enable human-hyaena coexistence.

3.3. Methods

3.3.1. Semi-structured interviews

I conducted face-to-face interviews to examine the views of people living in and around the Soutpansberg Mountains. Interviews were semi-structured with initial starting questions and broad topics predetermined (Crang and Cook, 2007). Semi-structured interviews are partially structured and partially unstructured, allowing for fluidity and interactive exploration within an organised and purposeful framework (Aldridge and Levine, 2001; Cloke *et al.*, 2004; Gibson and Brown, 2009). The flow of the conversation is unique for each interaction and varies depending on the interviewee’s experiences, age, and vocation. This method increases the flow of the conversation and puts interviewees at ease (Valentine, 1997). If an informant granted permission, I recorded the interview using an audio recorder.

I piloted interviews in March 2013. The pilot study allowed me to understand cultural variations in the rapport between respondents. I trialled questions and gauged interviewees’ level of understanding, and determined how effective the wording of questions was at promoting discussion. I adapted questions following the pilot period and refined the wording to avoid bias (May, 1993; Saris and Gallhofer, 2007).

Between April 2013 and February 2015, I conducted a total of 112 interviews. I held a few interviews in public places but most interviews occurred in the home or on the farm of the interviewee. These locations were advantageous because I used visual cues to assist the flow of the conversation and interviewees occasionally offered to show me examples of problems on their farm or used props such as photographs and animal studbooks to explain their arguments. Interviewing in home environments can offer researchers an insight into the private lives of interviewees (Dickson-Swift *et al.*, 2007). I recorded my personal insights and observations in an ethnographic diary,

which I wrote as soon as possible after completion of the interview. The interviews aimed to gain information about respondents' backgrounds, land usage, experiences of human-predator conflict, and experiences of and opinions about hyaenas. I also explored the role that hyaenas play within stories, myths, songs, and rituals. Interviews consisted of a mixture of open-ended and closed, or yes/no, questions.

Interviews were targeted across five different groups (Table 3.1). I assigned an identifying code consisting of a letter indicating interviewee's group and a number to each interview, e.g. A01 is the first interview conducted with a member of group A.

Table 3.1 Characteristics of interview groups and number of interviews conducted per group.

Group label	Group characteristics	Number of interviews
A	Owners and managers of private land/nature reserves	37
B	Coloured members of the Buysdorp community	31
C	Black members of the Buysdorp community, also known as the Thlane	33
D	Traditional healers	3
E	Relevant informants who do not fit in the above categories	8
Total		112

Initial question structure was similar between groups A, B, and C to allow for comparison. Minor variations in the interview script explored specific cultural and geographical factors related to the groups. I developed an independent interview guide for traditional healers (group D) in order to extract information exploring their usage of animals. These interviews aimed to investigate traditional healing practices and identify how healers incorporate brown hyaenas within these practices. Group E includes additional informants with relevant expertise who are not members of the aforementioned categories. I interviewed these participants on an ad hoc basis with the aim of gathering pertinent background information to support wider understanding around the thesis' aims. I uniquely tailored each group E interview to the interviewee's background. Appendix 2 lists interview questions for groups A, B, C, and D.

Informants within categories A, B, and C were geographically separated (Figure 3.1). Within each geographic space, I employed snowball and convenience sampling to recruit further informants (Browne, 2005; Cloke *et al.*, 2004). Ethnographic fieldwork commenced with members of category A as I already established a rapport with many local landowners and managers. These relationships developed through my work with the Primate and Predator Project (PPP) in the year and a half I was resident in the study area prior to commencing ethnographic fieldwork. Starting with familiar contacts helped me develop my confidence as an interviewer and hone my skills in discussing sensitive topics before speaking to new contacts. These initial informants also acted as gatekeepers who introduced me to other suitable participants. The 37 category A interviewees discussed 39 properties that they either owned or managed. This land area totalled 75,839 ha (758.39 km²). Informants from groups B and C were resident within the geographic confines of the 11,000 ha (110 km²) Buysdorp community. I visited almost every house within the Thlane sub-community of Buysdorp due to group C's small population size.

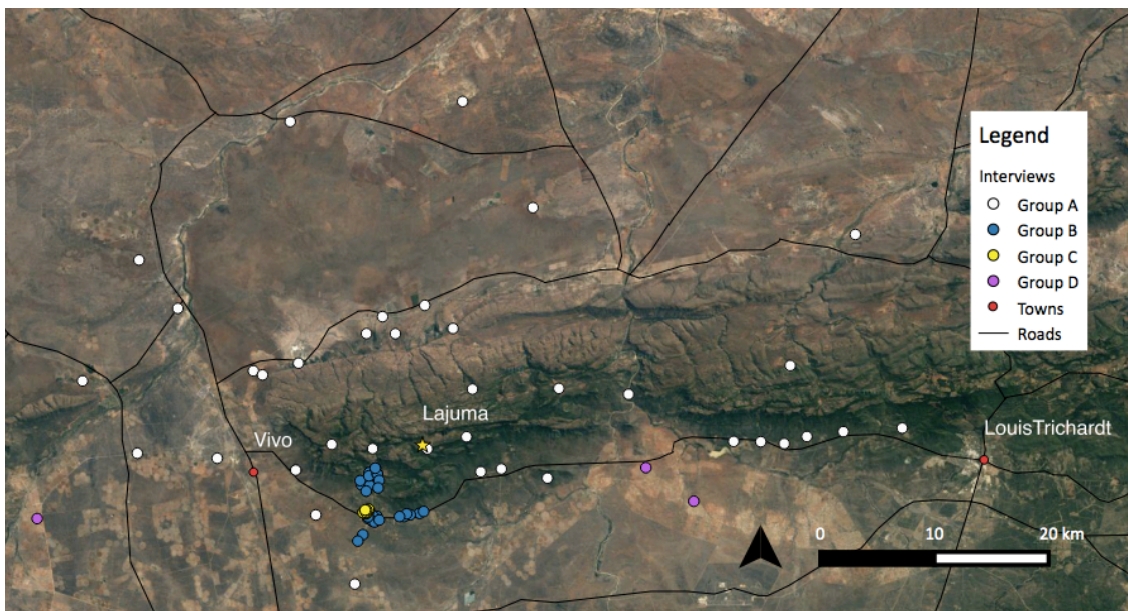


Figure 3.1 Map of interview locations conducted in and around the Soutpansberg Mountains categorised by group and in relation to Lajuma's location. Roads indicate tarred roads.

English was not the mother tongue of the majority of informants although some interviewees were comfortable conversing in English. I offered informants a choice to conduct their interview in English or in their native language. I led all English

interviews. If the interviewee opted for Afrikaans, Sepedi, or Tshivenda then I employed a local translator who accompanied me.

White South Africans are sometimes controversially classified as one of the 'tribes' of South Africa (Harrison, 1981). This 'tribe', although united by ethnicity, is bisected by linguistic and historical distinctions between Afrikaans and English speakers (Davies, 2009). I was concerned that the Afrikaners might extend reservations frequently applied to English-speaking South Africans to me.

Certain prejudices exist against female researchers as well. The majority of group A informants were native Afrikaans-speaking males. This demographic has a reputation for hyper-masculinity (Du Pisani, 2001). In my position as a British woman asking questions about masculinised topics of farming, land use, and wildlife, I felt the Afrikaans-speaking community might view me with distrust and suspicion. The masculine characteristics of Afrikaans farmers and hunters are strongly connected to paradigms of dominance over nature, survival in tough environments, and a romanticising of pre-Boer War rural life (Goodrich, 2013). They may thus be inclined to perceive an interviewer with a conservation agenda as being contrary to their worldview and treat them with suspicion. Informants may be less likely to answer sensitive questions truthfully if they believe that the interviewer is opposed to their lifestyle or will report illegal behaviour (Gavin *et al.*, 2010). I personally encountered playful ridicule for being a 'bunny hugger' or a 'greenie' while visiting local Afrikaans hunting bars and farms. In summary, my outsider position as a white, English-speaking, foreign female working for an organisation with conservation aims suggested that building trust and developing rapport might be a challenge.

I tried to compensate by developing and embracing insider characteristics. I learnt Afrikaans to a basic level, which created a positive first impression. Also my residency in the area prior to commencing interviews contributed to my reputation as trustworthy, non-judgmental, and sympathetic to the farmers' plights. Retrospectively, I believe that my positioning was not as clear-cut as I initially imagined. Despite my differences, there were circumstances when I was able to identify with respondents from an insider position, which I developed by working in southern Africa over many

years. My position also varied drastically based on my audience's background and how closely aligned their attitudes were to what they assumed mine to be. A study by Weiner-Levy and Quedar (2012) determined that insider and outsider positionality is not a static status and that sharing qualities other than indigeneness are equally important in building rapport. Rather than strive for complete objectivity, which is debated as potentially impossible or undesirable (May, 1993), I approached analysis of my ethnographic data with an awareness of my ambiguous positions in relation to my various informants and the advantages and disadvantages associated with them.

The presence of a local person helped to compensate for my status as an outsider. This was especially significant with the land-owning Afrikaans-speaking public (group A) and the Thlane community (group C). By giving people the option to converse in the language of their choice, I did not appear Anglo-centric. The presence of a translator who is local and is trusted helps researchers gain access to informants, build trust, and remove suspicions (Lewis and Phiri, 1998). My Afrikaans translator was the daughter of a local farm owner. Her position as a resident, a white Afrikaner, and her father's respected status helped to reverse some reservations about my position and gain access to informants in groups A and B. As two young females, we also appeared unthreatening when visiting people's farms. We dressed informally and strictly adhered to ethical considerations by always gaining permission (refer to Chapter 2 for ethical considerations). Within the Thlane community, I employed a young black male member of the society who was fluent in English, Tshivenda, and Sepedi. He also had strong command of Afrikaans and Xitsonga languages. He was born in the community and knew every Thlane member personally.

The benefits of having a local translator in attendance outweighed the few disadvantages of their presence. As the lead researcher, I found it difficult to fully engage with the interviews if they were not conducted in English. Semi-structured interviews allow the interviewer to improvise and expand upon interesting ideas as and when they arise (Crang and Cook, 2007). When interviews were being conducted in a language I did not understand I relied upon my translators to make important judgment calls on when to stray from the interview guide. I trained my translators in advance on what key topics or phrases warranted additional exploration but when

reading the translated interviews there were several times that I felt the opportunity for a valuable discussion was missed.

3.3.2. Participant observation

Participant observation develops a close relationship between the researcher and their subjects through long-term interaction (Gobo, 2011). Through this process, the quality of data collected during fieldwork is improved and the interpretation of data is enriched (Dewalt *et al.*, 1998). Participant observation is a personal experience based on a researcher's predefined attitudes and perceptions (Gobo, 2011). It combines participating and observing people as a means to conduct behavioural analysis and record information (Dewalt *et al.*, 1998).

I interacted with the white Afrikaans community and the communities in Buysdorp. I attended a biltong hunt and a game auction to develop my understanding of game farming. I regularly spent the night on Afrikaans landowners' farms while I was conducting my camera trapping survey. This enabled me to speak to private landowners informally over meals and to observe their farming practices and home environments. In the Buysdorp community, I observed how villagers interacted with their domesticated animals and how they managed their land in response to the threat of predation. I spent time informally amongst the Buys people attending social functions, volunteering at the school, and helping with physical labour on mixed farms. I attended community meetings, chatted to people waiting to be seen at the clinic, and mingled with departing churchgoers. I was interested in understanding how both groups spoke about and interacted with domestic and wild animals, with a particular interest in brown hyaenas and predators. I engaged with community members from differing vocations, genders, ages, and economic circumstances to determine relevant factors defining relationships with brown hyaenas and other secretive animals. Participant observation allowed further engagement with the cultural and symbolic nature of hyaenas in history, stories, and rituals.

I tried to embody the elements recommended for a successful ethnographer in participant observation by De Walt *et al.* (1998). I was non-judgmental and open to new experiences. I endeavoured to be a good listener and a careful observer. Language was a limitation of my participant observation experience (Crang and Cook, 2007). Constant translation can disrupt the natural flow of the participant observation experience. In a relaxed setting, communication is less regimented, and without fluency in the local language the true gist of an exchange can become lost in translation (Crang and Cook, 2007). Due to my limited understanding of Afrikaans, ignorance of the tribal languages spoken in the Thlane community, and my inconsistent exposure to these languages, revelations from my participant observation experience were limited to visual cues, auditory exchanges in English, and sometimes in Afrikaans. Nevertheless, the data acquired was worthwhile and in depth.

My positionality, as previously discussed in section 3.3.1, was exceedingly relevant throughout the participant observation process where the definition of the term 'participant' is sometimes questionable (Crang and Cook, 2007). Unlike studies relying solely on this methodology, my presence in the communities or on privately owned land was not constant because of my commitments to the other aspects of this interdisciplinary research. I visited Buysdorp and private properties frequently throughout the two-year fieldwork period, which helped to develop a long-term relationship and establish myself as a reliable and trustworthy observer. However, my unavoidable absences limited the depth of my investigation to an extent.

I recorded participant observation impressions and personal reflections in a handwritten ethnographic diary. Notes integrated the six layers for inclusion suggested by Cloke *et al.* (2004) (Table 3.2). Recollections can become skewed and important details or feelings forgotten if field-noting is not included in a regular daily regime (Crang and Cook, 2007). I recorded experiences as soon as was feasible to capture fresh perspectives.

Table 3.2 Six layers of description in ethnographic note-taking. The layers progress from outside to inside perspectives. From Cloke *et al.* (2004, p. 200).

Layer	Defining characteristics
1	Locating an ethnographic setting
2	Describing the physical space of that setting
3	Describing others' interactions within that setting
4	Your participation in interactions in that setting
5	Reflections on the research process
6	Self-reflections

3.3.3. Data analysis

Data was considered either quantitatively, qualitatively, or both depending on the type of information given. I utilised quantitative analysis for information such as predation levels which had measurable numerical or categorical outcomes (Bryman, 1988). All unquantifiable social data was assessed qualitatively (Gibson and Brown, 2009). Through the integration of quantitative and qualitative social data, I considered and compared concepts across different scales (Bryman, 1988).

I primarily summarised trends within groups using qualitative data. I discussed these trends against impressions of information gathered from various sources. I interpreted qualitative data using theme identification (Gibson and Brown, 2009; Ryan and Bernard, 2003). I selected themes using an inductive approach – selection based on their prevalence and importance within the empirical data – and an *a priori* approach – selection in relation to prior knowledge of the topics broached (Ryan and Bernard, 2003). A bottom-up grounded theory investigation of the social data determined this thesis' postcolonial approach to data.

I inputted transcripts from interviews and my ethnographic diary into NVivo v 10.2 (QSR International, 2014). I reviewed all documents within NVivo and coded thematically using the free node function. In NVivo, a node is a categorisation tool, which can be assigned across concepts, people, ideas, and places to link them conceptually (Lewins and Silver, 2007; Richards, 1999). I structured interview transcripts by level within Microsoft Word prior to uploading to NVivo. I initially

ascribed first-level coding to phrases or sentences within the interview dialogues which defined overarching ideas and recurrent themes in the qualitative dataset (Miles and Huberman, 1994). Selective or pattern coding followed to enable exploration of ideas and relationships between nodes at a finer scale (Miles and Huberman, 1994). I used the autocoding function in NVivo to produce tree nodes pertaining to each question which enabled response comparison across interviewees (Richards, 1999). I revised nodes throughout the organisational process as I gained a greater understanding of recurring themes.

I deconstructed and reconstructed themes within an ethnographic context and presented these as ethnographies within a realist/confessional framework, which aimed to intertwine culture and fieldwork (Van Maanen, 2011). Through the stories, opinions, and experiences of people living in and around the Soutpansberg Mountains, I explored wider political, psychological, and environmental constructs against a postcolonial backdrop.

3.3.4. Introduction to interviewees

The study area is composed of a dynamic mixture of people from different socio-economic backgrounds and ethnic groups. Although categorisation was necessary to understand the commonalities between the groups of interviewees and interpret data in relation to the assigned groups, every person has a unique story, which crosses boundaries of generalisation and cannot always be neatly summarised (Snape and Spencer, 2013). I acknowledged outliers and discrepancies between group members through deviant case analysis (Lewis and Ritchie, 2013) yet when required, I approached each group as a whole in order to examine data within a wider context.

I conducted participant observation and interviews with three main groups, which were defined by the geographic area they occupied and their cultural similarities. These groups (A, B, and C) are first referred to in section 3.3.1 and mapped by their geographic location in Figure 3.1.

Seldom do the members of groups A, B, and C mix in a social context. This is attributed to a culture of informal segregation, which hones social interactions to members of the same ethnic identity and is often observed in South Africa (Dixon and Durrheim, 2003; Durrheim, 2005; Finchilescu and Tredoux, 2010; Lemanski, 2004; Walker, 2005a). The community of Orania in the Northern Cape Province, South Africa, is an extreme example of this. Orania is an Afrikaans-only bounded territory, which embraces ideologies of an Afrikaner volkstaat (Hagen, 2013). Within my study area, geography and ethnic identity divide groups but boundaries are more blurred than Orania's more impenetrable approach. For example, the Buys (coloured members of Buysdorp) and the Thalane (black members of Buysdorp) live in the same community, however the Buys who are more numerous occupy a wider proportion of the community's land and the Thalane only occupy about 20 ha (0.2 km²) of geographically segregated land. The Thalane have a separate graveyard from the Buys. Most of the time they attend separate churches and they speak different languages.

Some Buys people resent the Thalane and feel threatened that the Thalane might attempt to assume control of Buysdorp. Conversely, other Buys people expressed that the Thalane are an integral and equal part of their community. Buys and Thalane children attend the same primary school (Mara Primêre Skool). However beyond interaction at an early age, social mixing between the Buys and Thalane is frequently limited to an employer/labourer relationship.

Hereafter I introduce groups A, B, and C in depth.

3.3.4.1. Group A: owners and managers of private land/nature reserves

Interviews were conducted with 37 people in group A. The majority of respondents were white apart from one coloured and one black respondent. They owned or managed 39 comparatively large tracts of land ranging in size from 3.2 km² to 93.6 km². The total area of land discussed by group A respondents summed 819.02 km². These properties were widely spaced across the study area; and were located north of the mountain (Limpopo Valley), on the mountain (Soutpansberg Mountains) and south

of the mountain (lowveld). Some of the owners interviewed do not live on their farms. Instead, they live in metropolitan areas and intermittently visit their properties which are either kept as holiday retreats or side-businesses. Because of the large area of land this group controls, they greatly influence how wildlife is managed in northern Limpopo Province. Most properties farm game either for hunting, tourism, breeding, or personal enjoyment (n = 33), although game farming might not be their primary land use. Many group A respondents use their land for multiple purposes and respondents ranked how their land is used (Table 3.3).

Table 3.3 Land use by group A respondents. A couple of interview numbers are listed twice (A27 and A28) to represent land usage on two separate properties owned by the same interviewee.

Interview number	No 1 land use	No 2 land use	No 3 land use	No 4 land use
A01	Cattle farming	Game farming	Vegetable farming	Tourism
A02	Tourism	Game farming		
A03	Personal enjoyment			
A04	Tourism	Personal enjoyment		
A05	Livestock farming	Hunting		
A06	Cattle farming	Tourism	Game farming	
A07	Hunting	Game farming	Cattle farming	Tourism
A08	Tourism			
A09	Tourism			
A10	Cattle breeding	Tourism		
A11	Education			
A12	Tourism	Hunting		
A13	Cattle and sheep farming	Vegetable farming	Tourism	
A14	Hunting	Tourism		
A15	Personal enjoyment	Cattle farming		
A16	Hunting	Game farming	Sheep farming	
A17	Personal enjoyment			
A18	Hunting			
A19	Cattle breeding	Game farming	Hunting	
A20	Salt mining	Tourism	Hunting	
A21	Livestock farming	Game farming	Hunting	Vegetable farming
A22	Tourism			
A23	Tourism	Hunting		
A24	Game breeding	Personal enjoyment	Hunting	
A25	Cattle farming	Hunting		
A26	Personal enjoyment			
A27	Hunting			
A27	Cattle breeding			
A28	Game breeding	Hunting		
A28	Cattle breeding			
A29	Cattle breeding	Vegetable farming		
A30	Cattle breeding			
A31	Vegetable farming	Hunting	Livestock breeding	
A32	Livestock farming	Vegetable farming		
A33	Education			
A34	Livestock farming	Game farming	Hunting	Vegetable farming
A35	Hunting	Game farming	Tourism	Vegetable farming
A36	Cattle breeding	Hunting		
A37	Cattle farming	Hunting		

The majority of respondents spoke Afrikaans as their native language (n = 27). English was the second most common native language (n = 7). The black respondent was a native Sesotho speaker. Two landowners hailed from Europe with German or Norwegian as their mother tongue, although they comfortably conducted their interviews in English.

I specifically targeted people with knowledge about their land in order to extract accurate information on conflict levels with brown hyaenas and other predators. These people either owned or managed the properties discussed. There was an extreme gender divide amongst people in these positions with only four female interviewees.

Group A respondents had the highest level of education - 86.5% of respondents completed 12 years of schooling or more and no respondents had less than six years of schooling. Many progressed onto higher education with several respondents holding medical or veterinary diplomas and one respondent with a PhD. The average age for Group A respondents was 48 years.

Group A did not have as strong a sense of community or cohesion as the other groups. The geographic separation between farms and the diversity of independent land management techniques engendered a culture of fending for oneself.

3.3.4.2. Group B: coloured members of the Buysdorp community, referred to as the Buys

Buysdorp is 110 km² property composed of four farms (Buisdorp, Mara, Buisplaats, Buishoek); one of which is leased to a commercial landowner (Figure 3.2) (de Jongh, 2004). There are 361 Buys people in residence (estimate given at Buysdorp committee meeting on August 12, 2013). Money from the lease funds some costs the community incurs. In addition, Buys residents pay an annual levy of 60 South African Rands to cover eventualities like broken water pipes. A large proportion of Buysdorp lies on the southern slopes of the Soutpansberg Mountains and is unmanaged.

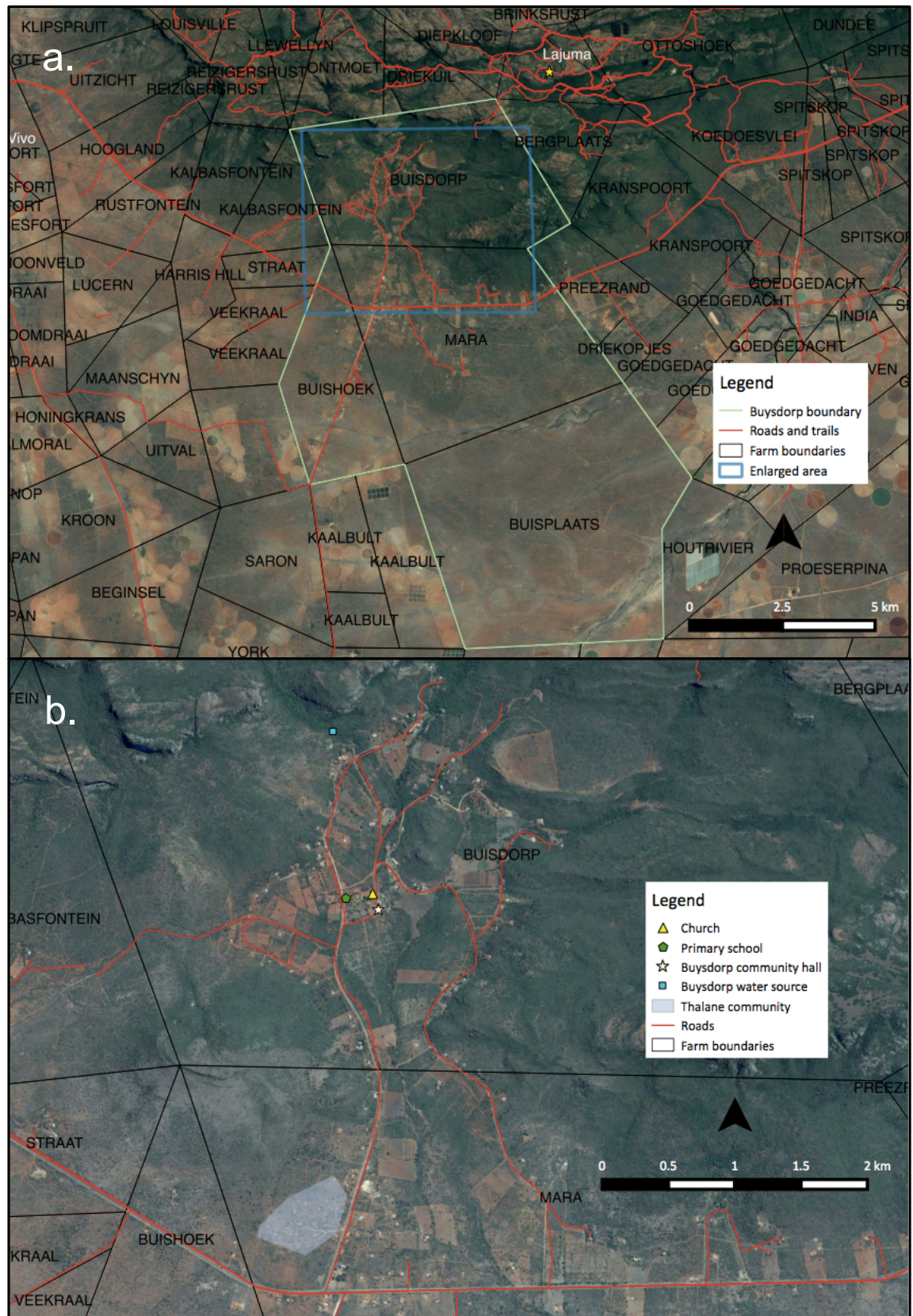


Figure 3.2 Maps of Buysdorp. a. The Buysdorp community in relation to Lajuma's location and featuring the four farms within Buysdorp's borders. b. Enlarged view of the central part of Buysdorp indicating where the Thalane community is located.

Buysdorp is semi-autonomous and is managed by a committee of five elected officials who make decisions for the community. The Buys are largely excluded from the wider government. Residents do not pay taxes and Buysdorp is charged lower governmental fees than other private properties. Two African National Congress (ANC) representatives based in Louis Trichardt represent the Buys' interests in the provincial government.

There are few employment prospects for young people in Buysdorp. Young people often drop out of school or turn to drinking and drugs. Some young people expressed a desire to leave the community because it is 'boring'. Often members of Buysdorp leave the community after school to work in urban centres like Johannesburg and then return to Buysdorp upon retiring. Many returnees said they were very happy to be back home. Consequently, the majority of the residents are older. The average age of interviewees was 59 years old. The majority of respondents (71%) were 50 years of age or older.

The Buys have a strong sense of identity and belonging. The Buys' native language is Afrikaans and they are coloured. Many Buys are direct descendants of Coenraad de Buys. Positive ancestry was confirmed by a DNA-genetic testing project led by the University of Witwatersrand and the University of South Africa. Members of the community enthusiastically volunteered to be tested to reconfirm their sense of identity (de Jongh, 2007). To become a resident of Buysdorp and claim a plot of land, applicants must prove to the committee that they were born in Buysdorp, married a Buys, or are a descendent of a Buys (de Jongh, 2007). The Buys' collective nature is reflected in how they refer to their community as 'die plaas' (the farm); they view Buysdorp as one communally owned farm rather than many independent plots belonging to individuals.

Plots are generally 0.2 km² but some Buys are granted larger plots (around 0.5 km²) if they conduct farming (Figure 3.3). The Buys also have a system whereby the plot holder 'owns' or takes stewardship of the natural mountainous area behind their land. Most Buys do not own livestock but those who do possess small herds (average size 33 animals) rather than the larger numbers kept on group A farms (average size 93

animals; however one farm managed as many as 700 head of cattle). Livestock generally is not interviewees' most important source of income and animals are often kept for personal use. Most Buys and Thalane people do not farm or use their land commercially to the same extent as group A respondents. Therefore, within these two areas I targeted a broader demographic which consciously included a mixture of men and women. Due to a greater collective mentality amongst the Buys and the Thalane, which is not present in group A, I considered opinions from across the communities to gauge perceptions and experiences of brown hyaenas and other predators.



Figure 3.3 Buysdorp from above showing an area where group B respondents live and average plot size. Houses are built from permanent materials on allocated plots. Plots are spaced apart to provide privacy and prevent overcrowding. Residents keep the land within their plots relatively natural aside from housing.

I conducted 30 interviews with Buys people and one focus group with four Buys women, bringing the total number of people interviewed to 34. Twenty were male and 14 were female. The people I interviewed were all coloured native Afrikaans speakers. The majority of Buys interviewees had completed 10 years of school. Only four respondents had progressed to higher education.

3.3.4.3. Group C: black members of the Buysdorp community, referred to as the Thalane

Although the Thalane people are members of the Buysdorp community, they are excluded from the decision-making committee and are not entitled to all the same rights as Buys people. The Thalane are not allowed to hunt while Buys people can apply for a permit from the committee in sanctioned hunting seasons. Subsequently, and possibly because they are not entitled to pursue legal avenues, there is a perception that the Thalane conduct more illegal hunting using snares or dogs. Another example of differing conditions is access to water. All Buys constantly have free-running water, which is sourced from springs in the Soutpansberg Mountains and is stored in individual water butts, but in Thalane there is only one water line for the whole community and they lack proper storage facilities. Sometimes the water is cut off and there is no water in Thalane for up to two weeks. This division of privilege illustrates the superiority complex of some Buys over black people (Ebersohn, 2012).

Fifty-nine people are resident in Thalane (S. Nalana, pers. comm.) and they occupy a very small portion of Buysdorp's land, which seems to be hidden away. Their namesake, a hill named Thalane, separates the northern boundary of the community from the rest of Buysdorp. Tar roads roughly form the southern and eastern boundaries (Figure 3.2), however Thalane dwellings are not visible from the roads; either trees or Buys houses block them from view.

The Thalane population was higher prior to the 1960s. During apartheid, members of the community were translocated into cultural homelands and following reconciliation, numbers never returned to a pre-apartheid state. Nowadays, some members of Buysdorp express concerns that the Thalane seem to be recruiting more people. There is some talk of building Buys stands around the Thalane area to enclose them further and prevent expansion.

The average home and garden in the Thalane covers 0.0023 km². Thalane plots are more closely spaced together than Buys plots. The Thalane are not allowed to build permanent structures (Figure 3.4) because historically they were brought onto 'die

plaas' as temporary workers for the Buys. Until 1994, they only had a prefabricated school which sat adjacent to the Buysdorp's primary school within the same grounds (de Jongh, 2006). Some Thalane argue that through their tribal roots, they have a more established claim to the land than the Buys and they therefore should be entitled to greater rights or ownership of Buysdorp (de Jongh, 2007).



Figure 3.4 Homes in the Thalane community, Buysdorp. Houses are mostly built from non-permanent materials as is decreed by the Buysdorp committee. Houses use traditional mud brick building techniques, which are cheap and easy to construct. Residents often remove all natural vegetation from the areas surrounding their homes.

The Thalane are black and speak a mixture of languages. There is a big variation in the tribal background of respondents. Sixty-seven per cent of respondents speak Sepedi as their home language. Thirty per cent of respondents speak Tshivenda and only 3% speak Xitsonga. Despite these cultural differences there seem to be no obvious divisions within the community. This may be because of the small size of the community and also because most black South Africans are multilingual, reducing challenges in communication.

I conducted 33 interviews in Thalane with 17 males and 16 females. The average age of respondents was much lower than the Buys sample, at 39 years. The community is composed of a greater proportion of young people than the rest of Buysdorp, many of which are unemployed females. The Buys trend for young adults to move to urban centres is less prevalent. The education level in Thalane is also lower. Interviewees had an average of six years of education. Five people had no formal education and conversely, only five people had completed 12 years of school.

3.3.5. Interpreting truth and methodological triangulation

From an ethnographic stance, facts are personal interpretations derived from “partial truths, partisan perspectives, and problematic modes of asking questions” (Goodall, 2000, p. 92). Basing knowledge around ‘partial truths’ does not make it fiction; it may make one’s understanding more real, more human, and less assumptive because it is free from the supposition that culture can be viewed as a scientific object (Clifford, 1986).

Determining attitudes towards carnivores and the effect this has on people’s behaviour can be challenging when compounded with the illegality of retaliatory behaviour (Goodall, 2000). Accessing sensitive information about animals was eased in one study using a randomised response technique which allowed respondents to convey information without admitting to any illegal or unpopular behaviour or beliefs hence reducing the feeling of judgment and the need for concealment (St John *et al.*, 2011). I used more traditional social science methods – interviews and participant observation – which had independent limitations.

Sometimes commercial landowners (group A) backtracked or dodged questions about sensitive issues. I sensed that they were concealing information to protect themselves. This behaviour supports the three S’s of illegal hunting – shoot, shovel, shut up – and has been observed in connection with the hunting of European wolves (Liberg *et al.*, 2012). Consequently, I am not convinced I gained a true picture of illegal activity

towards wildlife. On occasion, I was told stories about illegal poaching or hyaena damage informally off the record and a contradictory story during the interview. An audio-recorder is a constant reminder that all dialogue is public property and this can transform interviewees into 'actors' (Hull, 1985). Interviewees readily told me about named neighbours killing hyaenas but when I met the neighbour, they denied these accusations, implying that one of the two respondents was untruthful. The neighbour would perpetuate the cycle by incriminating another neighbour who in turn would deny illicit activity.

Group B and C respondents are more open about their relationships with animals because they own less livestock and game, therefore they have fewer problems with predators. As a result, they probably do not kill predators as frequently. Additionally, with lower education levels and less experience acquiring government issued animal permits than commercial farmers, they are probably not as aware about legality or illegality regarding wildlife, thus producing more candid dialogues.

Careful wording and deliberate omissions are not the only ways to craft an inaccurate representation of the truth. Inaccuracies may be presented because of innocent ignorance of the 'universal knowledge' of science (Rabinow, 1986). Much ethnography strives to ascertain and appreciate a person's personal truth without questioning it against scientific reasoning (Goodall, 2000). This thesis crosses disciplinary boundaries and compares local interpretations of hyaenas with biological truths, thus necessitating consideration about the accuracy of scientific fundamentals. Some people resolutely stated that brown hyaenas kill their livestock but they backtracked when I asked whether they were certain that brown hyaenas were culpable. They revealed that they found carcasses with hyaena tracks nearby and made an assumption of blame. Respondents told me that the aardwolf (an insectivore (Stuart and Stuart, 2007)) and bushbabies (primarily frugivores and insectivores (Stuart and Stuart, 2007)) kill small stock. Some interviewees said that they have seen brown hyaenas climbing trees. Ethological knowledge, which I am well informed about, renders these statements highly unlikely. My awareness of probable inaccuracies induced my scepticism towards all information acquired from these informants. I also relied on assumptions of a basic level of knowledge about hyaenas. For example,

commercial farmers gave accounts of hyaena spoor sightings but I did not test their proficiency in track identification. Domestic dog and spotted hyaena tracks can be easily misidentified as brown hyaena (Stuart and Stuart, 2003).

Several group B and C respondents gave contradictory statements by making it difficult to interpret their interviews cohesively. For example, a person might initially say that he likes brown hyaenas and later express that he does not want brown hyaenas on his land because they are scary animals. This may reflect confusion about the questions or a lack of clarity in which factors truly define an attitude (Williams, 2011).

In the Buysdorp and Thlane communities, many people were older or admitted that their eyesight is poor. This may have affected the accuracy of their answers to the photo identification questions, thus eliciting inaccurate assessments on predator knowledge.

Although methodological limitations have been identified, by acknowledging these and triangulating methodologies I was able to evaluate the information I received alongside omissions, consider dialogue and experiences at a full sensory level, and reinforce my understanding (Lewis and Ritchie, 2013). Method triangulation compares results from multiple methods during the evaluation process (Baxter and Eyles, 1997; Gibson and Brown, 2009). Convergence of results across methods improves the credibility and dependability of results (Baxter and Eyles, 1997). Incorporating participant observation with interviews triangulated results, which strengthened the validity of my study (Aldridge and Levine, 2001; Baxter and Eyles, 1997).

3.3.6. Predator identification

To aid dialogue and test respondents' predator identification skills, I showed group B and C interviewees photographs of ten South African predators and asked them to identify the animals and tell me about them in a local context if present (Appendix 3). Group A respondents were not formally tested because it was clear from their

dialogue and their use of predator photographs made available during the interview that they had an almost perfect knowledge of predator identification. In Buysdorp (n = 30; the focus group with four women was excluded because it was impossible to distinguish individual knowledge), the species pictured in 54% of photographs were identified correctly when using general names for species such as jackal for black-backed jackal and hyaena or wolf for brown hyaena. Men scored higher at species identification (average score 61.5%) than women (average score 39%). Buys women are less involved with nature. No woman reported participating in hunting, for example. While many group B respondents could identify a hyaena (76.7%), only one respondent correctly stated the different names for brown and spotted hyaenas rather than referring to both species using the generalised terms of hyaena or wolf. Misidentification occurred frequently between leopards, cheetahs, and tigers (*Panthera tigris*).

The Thalane community (n = 33) was less proficient at predator identification with the species pictured in 44% of photographs identified correctly. Again, women scored lower (36.9%) than men (49.4%) but the gap between gender and predator knowledge was less pronounced than amongst the Buys. Only 40% of group C respondents could identify a hyaena at a non-species specific level.

Accuracy in identifying predators and hyaenas improved with age in the Buys community. This may be because the older respondents spent more time in nature and engaged more with farming than younger respondents. In Thalane, accuracy in predator knowledge was highest for respondents aged between 30 and 60.

3.4. Fieldwork reflections

3.4.1. Direct experiences of brown hyaenas

The brown hyaena's nocturnal habits and secretive nature disguise the species within a metaphoric cloak of invisibility. Their inconspicuousness has huge implications, both

positive and negative, for their relationships with people in and around the Soutpansberg Mountains.

I asked all interviewees about their cultural connections to brown hyaenas. Within the Thlane community, this led to discussions about hyaenas' roles within witchcraft and traditional medicine. When I asked questions pertaining to witchcraft and traditional medicine to the predominantly white commercial landowners, the response was often accompanied with scoffing or a rolling of the eyes indicating that these were foolish questions. It was clearly indicated that spiritual beliefs associated with animals were reserved exclusively for the black population. However, many commercial landowners inadvertently broke away from this attitude in their discourses about the invisibility of brown hyaenas. Because brown hyaenas are quiet and seldom sighted, several group A interviewees referred to them as ghosts or ghostlike.

"I see them as ghosts. They really are. We call them ghosts because they are around but they are so unobservable and their ranging seems to be so wide. You hardly ever see the things even though they are very present." [A03]

Commercial farmers spoke of the brown hyaena's magical quality, which allows them to be ever present yet remain largely concealed.

"I don't like the spotted hyaenas, but that hyaena is a special hyaena; it's like magic." [A12]

Consequently, the white landowners implicitly imbue the species with a spiritual quality. The rarity of sighting a brown hyaena makes any interaction with the species special, memorable, and appreciated. Some ecotourism operators said that seeing a brown hyaena is a more valuable experience for their tourists than seeing a leopard, an elusive 'big five' species (Lindsey *et al.*, 2007). One hunting outfitter did not offer brown hyaena hunts because he could not guarantee a trophy for clients due to brown hyaenas' scarcity and how difficult they are to hunt. Even some landowners who experience problems with brown hyaenas said they would not kill one due to their

perceived scarcity. Therefore, brown hyaenas' 'magical' elusiveness earns the species respect in some farmers' eyes.

Commercial landowners who live on their properties are very informed about and involved with their land, yet some have never seen a brown hyaena or only had one brown hyaena sighting in 40 years despite seeing signs such as tracks or scats regularly. Although brown hyaenas are seldom sighted, 78% of commercial landowners or managers have seen one on their land at some point.

The brown hyaena's invisibility is interpreted differently amongst the Thalane community. The hyaena's elusive nature is construed as magical but this is viewed with suspicion rather than awe. In the Thalane community, the mysterious nature of the brown hyaena is interpreted as a malicious, untrustworthy, and powerful quality. The elusiveness of the animal perpetuates negative perceptions and increases fear.

More Buys and Thalane people than anticipated reported having physically seen a brown hyaena (50% and 18.18% respectively), although many of these 'sightings' were of dead animals killed by cars or snares. I believe some of the accounts are cases of incorrect identification. One man reported that while hunting, his dogs (*Canis lupus familiaris*) chased a hyaena in the middle of the day and it climbed into a tree to escape. As hyaenas are nocturnal and not known to climb, I doubt the validity of this report. A woman reported that she often sees brown hyaenas eating fruits when she gathers wood in the mountains, especially in summer. Biological information on the species' diet and secretive habits indicate that this report is almost certainly a case of misidentification. The remainder of sightings (n = 10) are more likely to be accurate. One brown hyaena was found dying in a snare. Two of the sightings were of dead hyaenas found as roadkill. One person recounted hitting a hyaena with his car at night. The risk of road traffic accidents for hyaenas is a recurring theme, which was brought up by all three groups and also in interviews with traditional healers. This indicates that roads may be a larger threat to the species locally than previously considered.

3.4.1.1. Experiences of coexistence

Throughout the dialogues about brown hyaenas, landowners and community members repeated variations on a single phrase:

“If hyaenas don’t bother me, I don’t bother it.” [A13]

This sentiment seems to justify negative behaviour taken against brown hyaenas or other large predators and imply that ‘naughty’ animals deserve punishments. This concept also infers that the landowner or community member is reasonable and willing to give predators a chance as long as they *“mind their p’s and q’s”* [A16]. There appears to be an imaginary line of what is considered acceptable behaviour for brown hyaenas, although standards are not the same across the board.

Ecotourist operators are the most relaxed and do not consider any hyaena behaviour unacceptable. Ecotourism ventures stock their land with expensive game animals such as sable (*Hippotragus niger*), giraffe (*Giraffa camelopardalis*), and blue wildebeest (*Connochaetes taurinus*). Leopard and brown hyaena are accused of killing the young of these species incurring the ecotourist operators considerable financial losses but this is viewed as acceptable and natural behaviour.

One ecotourist operator who loses an estimated 75% of all wildebeest and 70% of all zebra born annually to leopard predation said:

“You know we love seeing the leopard and to live with the leopard. We have to have a balance and the balance is that you let it eat.” [A02]

He expressed a similar acceptance level towards brown hyaena although he did not believe that they were killing his game.

Although livestock farmers are less inclined to be as accepting to predation, some expressed nature-centric mentalities. One livestock farmer said:

“I like hyaenas because they are part of the package on the farm. When you are farming you take something out of nature and to live with wild animals is a balancing mechanism.” [A01]

People often acknowledge that brown hyaenas have to eat and that they are merely trying to survive. However in many cases, the way in which a predator fulfils its survival instinct and whether the practice benefits or disadvantages humans defines whether it is displaying acceptable behaviour or not. Certain predators are unpopular and consequently persecuted based upon a dislike for their hunting and eating practices. Cheetahs and African wild dogs are condemned for hunting almost daily because this behaviour is construed as greedy and farmers believe these species cause a greater level of damage than larger predators. Larger predators such as leopards that only need to kill every few days (Estes, 1991) are respected for their less wasteful restraint. One game farmer dislikes brown hyaenas because of their scavenging habits. On his farm, he observes them displaying dominance over leopards by stealing their food. Kleptoparasitism causes the leopards to hunt game more often than they normally would have to.

“In the beginning when I saw them (brown hyaenas) on the game farm, I was so thrilled to know there is brown hyaena around and now I’m starting to get a bit pissed off with them because of the predation factor on the game.” [A27]

The commercial landowners are the most educated group of interviewees and many of them understand that brown hyaenas are predominantly scavengers. It is only on rare occasions such as the example above that commercial farmers view scavenging as negative behaviour. Brown hyaenas are frequently commended for clearing carrion on game farms. Many game and cattle farmers have vulture restaurants on their properties where they deposit carcasses of dead animals (Yarnell *et al.*, 2014). The brown hyaena’s role in cleaning up the farm and stopping the spread of disease is appreciated.

The Buys and Thlane people did not generally view scavenging in a positive light. Some Buys people call brown hyaenas ‘totsis’, a negative South African term for thief

or criminal, because they steal from other animals. Equating scavenging to thievery reinforces the conception that hyaenas are untrustworthy and that they are not behaving according to human-constructed standards.

Most farmers who believe that brown hyaenas are actively hunting on their land perceive this as unacceptable behaviour, which warrants retaliatory responses. However, one commercial farmer likes brown hyaenas because an individual on his land kills problem predators including the widely disliked black-backed jackal.

“I like brown hyaenas. I have a mother that raised young. I can’t remember the exact numbers but I think she killed 14 jackals, three caracals, one civet, and one honey badger. That’s what she killed around the den, all that stuff I will show you.” [A34]

The farmer showed me the den site (Figure 3.5). I identified remains from one common warthog (*Phacochoerus africanus*), two common duikers, one blesbok (*Damaliscus pygargus phillipsi*), one honey badger, 12 jackals, two caracals, one African wild cat, one African civet, one cow calf (*Bos taurus*), one impala, one cape porcupine (*Hystrix africaeaustralis*), and one steenbok (*Raphicerus campestris*) around the den’s two entry holes. Even after placing a camera trap by the den for two months, it was indeterminable whether the brown hyaenas killed or scavenged the mesopredators. Most studies analysing brown hyaena diet found little evidence of terrestrial predator consumption (Owens and Owens, 1978; Siegfried, 1984; Stein *et al.*, 2013) or hunting (Mills, 1990). Regardless of the actual cause of the jackals’ death, the farmer’s version of the situation makes him appreciate brown hyaenas. It softened the cattle losses he experienced when brown hyaenas grabbed calves from his birthing cows.



Figure 3.5 Carcasses found outside an active brown hyaena den on the property of a group A respondent north of the Soutpansberg Mountains. The central skull is from a honey badger. The skull on the lower right is from a black-backed jackal.

The definition of what is considered acceptable behaviour for a predator is often assigned to the animal's feeding and hunting practices and is defined by people at an individual level. The commercial farmers who display the greatest level of coexistence with wildlife take responsibility for their own role in the environment before judging a predator's behaviour. These farmers proactively protect their livestock through sustainable methods such as kraaling at night, moving young animals away from predation hotspots in mountainous areas, and guarding their herds. Consequently, they have very few losses to predation and many of these farmers are proud of this achievement. This pride hints that they feel like they have outsmarted nature's natural course. On the rare occasion when an animal is lost to predation, these farmers mostly blame themselves for the loss rather than the predator. One game farmer lost 20 ostriches (*Struthio camelus*) to brown hyaena predation yet he criticised himself because the habitat was not suitable for ostrich and as a manager he should have known better than placing them there. Another farmer lost a calf to leopard predation

but blamed himself because he was busy over the Easter holidays and forgot to lock up his herd.

Within the Buysdorp community, 62% of respondents own livestock or small stock and even though many residents are afraid of predators, losses are less impactful. Coexistence is common because owning livestock often represents an extra source of household income or food, rather than the main source. Additionally, coexistence is facilitated by a very accepting attitude towards nature and wildlife. Unlike many commercial farmers and Thlane members, the Buys accept that predators belong in the area.

“I told you already you will find it (the brown hyaena) in the mountains, we invade their privacy even I, really, we invade their privacy because they are staying in the mountains now we build our houses right in the middle of the mountain, so we invade their privacy.” [B04]

The mountains and its wildness are a strong part of the Buys’ identity. The Buys take pride in the beauty of the mountains and their coexistence with wildlife. Following a period of diaspora, Buys people feel a longing to return home and rejoin nature upon retirement. Despite life changes and relocations, the mountain and its animals always remain as a *“pillar of strength”* [B21], symbolic of their ancestral heritage and connection to the area.

3.4.1.2. Experiences of conflict

Acknowledging that the brown hyaena needs to eat and a place to live does not always excuse its behaviour when it jeopardises human needs, as illustrated by this farmer’s statement:

“Everything is just trying to get a bit of food in their belly but I just think they (brown hyaenas) are a problem to me because they are taking food out of my belly.” [A36]

Many farmers express a not in my backyard (NIMBY) mentality (Dear, 1992) towards predators on their land. They are supportive of the brown hyaena living in the wider area and accept that hyaenas need to consume meat to survive. However, as soon as a brown hyaena moves onto their land, the farmer no longer accepts the animal. At this point, the animal crosses the imaginary line of what is considered tolerable behaviour and becomes a 'bother'.

Brown hyaenas are oblivious to human expectations of predators and how unacceptable behaviour differs across landscapes. A hyaena can unknowingly pass between a property where its presence is welcome to a farm where it is considered a pest, therefore transitioning from being a 'decent citizen' to a 'bad animal' (Arluke and Sanders, 1996, p. 175). Farmers attribute anthropomorphic qualities to predators by expecting them to understand and adhere to human-defined rules of acceptable behaviour. This sets them up for failure and encourages conflict. Once a predator is perceived as a livestock killer or a threat to humans, it is branded as a 'bother' and consequently, in some circles it becomes socially acceptable to retaliate against it.

Although 32% of commercial landowners or managers experience problems with brown hyaenas, they are not always recognised as a serious pest because the frequency of hyaena conflict is lower and more isolated than problems with leopards. Leopards are identified as the most problematic predator and affected 58% of respondents. This finding is supported by previous social research on leopard conflict in the region (Chase Grey, 2011; Constant, 2014). Jackals and caracals are frequently identified as serious problem animals for small stock farmers. Strong antipathy towards and focus on more pressing predators and crop-raiders like baboons (*Papio ursinus*) partially shield brown hyaenas from negative perceptions and persecution, reinforcing their ability to move undetected. Unintentional blindness towards hyaena activity is comparable to the psychological condition whereby an observer cannot focus his attention on all aspects of a scenario and may unconsciously or consciously overlook the least important or least obvious (Mack, 2003; Simons and Chabris, 1999).

Eight livestock farmers in group A stated that they had experienced depredation from brown hyaenas. Livestock targeted by brown hyaenas includes cows, sheep, and goats. One livestock farmer witnessed seven brown hyaenas attacking a calving cow, killing the emerging infant, and eating the afterbirth. Several farmers blame brown hyaenas for breaking the legs of their livestock or biting their tails off. One farmer stated that the brown hyaena is dangerous to his calves due to the likelihood of infection around the bite site.

“...the brown hyaena comes and he bites it (the calf) on the neck at the back but he can’t hold it, he’s not strong enough so the calf jumps up and runs away but tomorrow morning that calf can hardly walk, his neck is so sore and that and then I mean he just stands there. If I don’t find him that day in the bush by tomorrow there’s infection in and by three days it dies from infection.” [A36]

Nearly half of the group A respondents who experience predation by brown hyaenas did not perceive the brown hyaena as a problem animal because the losses were few in comparison to leopard predation, the amount of damage was low, and attacks were infrequent. One farmer stated that the brown hyaena raided his watermelon and sweetcorn crops as well as killing his cows. By guarding his fields, crop damage is easily prevented and again livestock predation by leopards strongly supersedes hyaena damage on his farm, therefore directing his attention elsewhere.

Four game farmers or hunting operators knowingly lose wild animals to brown hyaenas. Game farmers are more accepting of losses than cattle farmers. They expect a percentage of their game to be eaten by predators regularly and demonstrate greater sympathy towards predator-prey relationships.

There is no game farming in Buysdorp and over half the informants are livestock farmers. About half of the people who farm with livestock or chickens experience losses from predators, mostly by leopard, caracal, and serval. Three farmers reported problems with brown hyaena. These losses are with goats, newborn calves, and older calves, but like the commercial farmers these incidents are mostly isolated. Only one

Buys farmer incurred considerable losses by brown hyaenas with six to eight calves killed in a short period.

Retaliatory behaviour against animals blamed for livestock losses and crop damage is common (Ikanda and Packer, 2008; Kissui, 2008; Ogada *et al.*, 2003; Romañach *et al.*, 2011), especially amongst people with negative attitudes towards problem animals or experiencing regular losses (Romañach *et al.*, 2011). Several commercial landowners admitted to killing brown hyaenas in the previous five years. Informants caught an estimated nine brown hyaenas in cages and killed them. One hyaena was shot on sight because the cattle farmer was concerned it might harm his livestock. More hyaenas may have been killed than were reported as interviewees might have concealed their actions to avoid admitting to unlawful behaviour.

Group A respondents euthanised three hyaenas because they were found injured by wire snares. The only brown hyaena killed by group B respondents was found in a snare and was shot. Snares are often set for *bushmeat* (section 1.3.3) but can indiscriminately kill bycatch (Becker *et al.*, 2013; Lindsey *et al.*, 2011b). Many group A and B respondents stated that snaring is becoming increasingly common. This supposition is supported by PPP observations of a high level of snaring amongst leopards with three global positioning system (GPS) collared individuals dying in snares between 2012 and 2015 (Williams *et al.*, in review-b). I found additional evidence of snaring during my camera trapping surveys.

Few Thlane own livestock and therefore depredation by brown hyaenas is seldom mentioned. Predator conflict is mainly ascribed to smaller mesopredators such as serval and jackal, which are accused of killing chickens. One interviewee described how his hunting dogs killed a brown hyaena in the mountains but this was a non-targeted attack. Another account revealed how a brown hyaena killed a hunting dog.

This comparatively low level of conflict by brown hyaenas is supported by damage-causing animals reports to the government. In the Vhembe district, about 10 damage-causing animal reports per year pertain to brown hyaena problems while about 30 are lodged for leopards (A. McMurtrie, pers. comm.).

3.4.2. Brown hyaenas in witchcraft and traditional medicine

One elderly female respondent from the Thlane community immediately recognised the brown hyaena from the photo provided and stated, *“It is not from this world.”* [C05]. A postgraduate student studying biological conservation at the University of Venda told me that even hearing the word for hyaena in her language invokes an eerie atmosphere.

“The moment you mention the word phele (the Tshivenda word for hyaena), you even feel it in your head that you are saying something strange, unusual. If in a gathering of Vendas you say ‘ehh phele yanga’ like ‘my hyaena’, oh man, that’s so wrong.” [E06]

Despite acquiring an understanding and appreciation of the brown hyaena’s role within the ecosystem and learning that this animal is not generally harmful to people, negative cultural associations with the species are still deeply rooted in the postgraduate’s perceptions of the animal. The Tshivenda term for hyaena, phele, is applied to all hyaenid species. Phele is also the Tshivenda word for a gravedigger; associations with death through scavenging or grave digging link the two definitions of phele. Many black respondents identified brown hyaenas as otherworldly. Many respondents across groups referred to hyaenas as wolves. One group A respondent nicknamed my translator and I ‘die wolve mense’ (the wolf people). A respondent in Buysdorp insisted that werewolves live near the community and the werewolf is the same animal as the brown hyaena.

Amongst respondents, negative imagery of the hyaena’s affiliation with witchcraft are almost exclusively limited to the black Thlane community and these. In South Africa, belief in ghosts and witchcraft are more closely associated with black rural communities than the more urban white Afrikaans-speaking people (McEwan, 2008). No white commercial landowners have any associations with hyaenas through witchcraft or traditional medicine but many of them spoke about their black staff’s beliefs. They expressed that their staff’s indigenous knowledge of animals was infantile and naïve. They said that the blacks would believe anything and used my

questions as a platform to distinguish and distance themselves from the local black population. This is similar to the way that colonialists used African beliefs in the occult as evidence of their irrationality and as justification for excluding these people from equal citizenship (Ashforth, 2005).

Within colonial ideologies, belief in witchcraft is an indicator of backwardness and colonial powers assumed that primitive notions such as these can be cured through civilisation, religion, and modernity (Brantlinger, 1985, p. 178). Reflections on the anthropology of witchcraft indicate that belief in the occult has not dissipated in postcolonial Africa. Instead, these beliefs have evolved and even increased in response to modernisation and inequalities stemming from European influence and capitalist principles (Apter, 1993; Auslander, 1993; McEwan, 2008; Niehaus *et al.*, 2001). Material possessions, wealth, and access to basic healthcare are unevenly distributed across society as a consequence of colonisation and the apartheid; dividing people and creating fears and jealousies that are manifested through ideologies of witchcraft or soul eating (Apter, 1993; Geschiere, 1997; Schmoll, 1993). Niehaus *et al.* (2001, p. 193) summarise experiences of witchcraft in rural South Africa: “For villagers witchcraft has less to do with civilisation and African identity than with their experiences of misery, marginalisation, illness, poverty and insecurity...”. Superstitious beliefs can be used to explain the inexplicable or compensate for unfortunate occurrences (Ashforth, 1996; McEwan, 2008). A prosperous or successful person who does not share their wealth and good fortune is often accused of witchcraft (Bastian, 1993). Accusations of witchcraft can reinforce social inequalities and legitimise desires (Niehaus *et al.*, 2001, p. 112).

A witch is loosely defined as a human being who is possessed with jealousy, greed, malice, and anti-social tendencies, and aims to harm the people around him or her using supernatural means (Ashforth, 2005; Hickel, 2014; Niehaus *et al.*, 2001). Witches are considered to be exempt from personhood due to their lack of moral and social being, and their ability to transition into animal familiars (Niehaus *et al.*, 2001). It is believed that witches secure their success by transforming their victims into diminutive zombies that work for them throughout the night (Geschiere, 1997; Niehaus *et al.*, 2001). Witches are believed to show mastery over the zombies who

have no free will or independent identity (Niehaus *et al.*, 2001). This relationship mirrors the domination of migrant labourers by European masters (Niehaus *et al.*, 2001). Through modernisation, it is believed that witches acquired new tools to conduct malicious acts more effectively (Niehaus *et al.*, 2001). Insecticides and chemical poisons, automobiles, and night trains can be used by witches as weapons or for transportation (Niehaus *et al.*, 2001).

The perception that witchcraft or superhuman powers can cause harm to members of one's community is commonplace in black South Africans (Ashforth, 1996; Kohnert, 2003; Niehaus *et al.*, 2001). Belief in witchcraft is especially prevalent in South Africa's most impoverished provinces of Limpopo and the Eastern Cape (Kohnert, 2003). Despite this geographic predominance in South Africa, examples from across Africa indicate that witchcraft beliefs span socio-economic classes, the urban / rural divide, and education levels (Apter, 1993; Ashforth, 2005; Bastian, 1993). Adam Ashforth's ethnographies describe witchcraft beliefs and practices in the urban setting of Soweto, South Africa (Ashforth, 1996, 1998, 2005). In Lagos, Nigeria, English newspaper articles describing witchcraft are extremely popular (Bastian, 1993). A literate elite who can afford to purchase newspapers and who can understand English will translate and retell the stories to eager listeners, thus illustrating how interest in witchcraft extends across societal groups (Bastian, 1993).

In the Thalane community, 73% of interviewees said that they believe in witchcraft. Some people believe in witchcraft because they heard about it from their elders or from *sangomas* (traditional healers). Several people believe because most of the people in the community believed, indicating a desire to be part of a shared knowledge. A couple of respondents had personal experiences of perceived bewitchment. One respondent believed he was bewitched and became mad until the *sangoma* healed him. A second interviewee stated that he knows there are witches because they are trying to 'take him' and pointed at white patches of skin on his hands. He suffers from the skin condition vitiligo whereby white patches of skin develop due to a deficiency in melanin (British Skin Foundation, 2015). Every month he visits the *sangoma* to counter the witchcraft that is being wrought against him. The

27% of Thalane respondents who do not believe in witches mainly hold strong Christian beliefs and are evenly spread across gender and age brackets.

Witches use animals in several ways: animals can indicate a witch's presence; animals can be the familiar of the witch; witches use animal parts as *muti* (traditional medicine) to transform the witch or to cast spells; and after death, the spirit of a witch can occupy an animal body and this animal will continue to spread wickedness (Morris, 2000a; Niehaus *et al.*, 2001).

Many people within the Thalane community recognise hyaenas as malevolent, unearthly animals. Other animals are assigned a similar stigma. Those earmarked for caution due to their associations with magic are often predators, nocturnal animals, or animals considered dangerous such as hyaenas, owls, cats, or snakes (Cumes, 2004; Niehaus *et al.*, 2001). A malevolent snake similar to the giant snake known as Inkosi ya Manzi (Ashforth, 1998) is described in the Thalane community and is commonly referred to as Dyambila. Dyambila is a giant serpent in Venda mythology that lives in the mountains and can kill cows or people by attacking the head and extracting the brains (Vhembe Biosphere Reserve, 2008). The Thalane respondents said they heard the stories of the Dyambila and of people who had been killed by it from their grandmothers. These respondents stated that they are afraid to walk in the mountains alone for fear of encountering the giant snake. The respect that younger people retain for older community members and the lack of outside information about wildlife mean that those who are exposed to these stories embrace them fully.

Associations between hyaenas and witchcraft are common across hyaena species and cultures (Frembgen, 1998; Glickman, 1995; Kesby, 2003; Niehaus *et al.*, 2001). Hans Kruuk said, "Undoubtedly, hyaenas play a more important role in African witchcraft than any other animal, and in this continent witchcraft is very commonly practiced" (1975, p. 49). In Africa, the animal most closely linked to witchcraft is the spotted hyaena and it is believed that witches ride on their backs casting spells, eat butter made from hyaena parts, or use the butter to fuel their torches (Kruuk, 1975, 2002; Morris, 1998). It is believed that witches can transform into hyaenas to attack livestock or humans (Morris, 1998).

Hyaenas are frequently connected with love magic and this is attributed to the unusual genitalia of the spotted hyaena (Frembgen, 1998). Male and female spotted hyaenas have visually identical genitalia. Female spotted hyaenas have an erectable penis-like clitoris and a pseudo-scrotum consisting of fibrous-fatty tissue (Funk, 2012). This 'impurity' is always a stumbling block towards societal acceptance of hyaenas and is responsible for accusations of hyaenas being hermaphrodites which change sex annually (Wilson, 2003). Although male and female striped and brown hyaenas possess distinctive genitals, they have not escaped similar beliefs (Funk, 2012). I did not record any associations between hyaenas, love magic, or sexuality in my interviews.

Witches are accompanied by an animal familiar, which can be commanded to attack their victims. It is commonly believed that the witches in and around Buysdorp walk with hyaenas or use their hyaena familiars as a form of transport, the '*horse of the witches*' [C25], and that witches can ride a hyaena to Durban and back in one night. Many of the Thalane people believe that witches can use hyaenas for transport, can transform into hyaenas, or are used for *muti* but they are very vague on specifics regarding these practices. Ashforth (2005) experienced a similar lack of detail while conducting ethnographic research about witchcraft in Soweto. He summed up this phenomenon by saying, "A witch is a witch. And only the witch knows how witchcraft works." (Ashforth, 2005, p. 65).

Several people said that witches and therefore hyaenas are not common in Thalane.

"This is a hyaena but here in Mara (the area around Buysdorp) you can't see it. When you can see this thing, it's a witch thing. There are people I think witch...you can't see it easily. You see it (the hyaena), they send it, something is wrong. We don't have such an animal here in Buysdorp." [C17]

Sangomas and people practicing witchcraft use plant and exotic animal parts as ingredients in traditional medicine to either promote or fend off the effects of witchcraft and evil (Cumes, 2004). Body parts of hyaenas are used for protection by *sangomas* (Kruuk, 2002; Morris, 1998). In Tanzania, it is believed that feeding livestock

hyaena skin, heart, or genitals will protect the cattle from predation (Kruuk, 1975, 2002). Hyaena parts are also consumed or rubbed on human skin for protection from witchcraft (Kruuk, 1975), to strengthen the body, improve fertility, induce dreaming, and protect from theft or allow a person to steal without being detected (Morris, 1998).

Although brown hyaenas are used for *muti* and are sold as traditional medicine at Johannesburg's Faraday Market (Whiting *et al.*, 2011), the demand for this species is smaller than that of the spotted hyaena (Mills and Hofer, 1998). In my study area, however, interviews with traditional healers and members of the Thalane community suggest that the brown hyaena has greater magical properties than the spotted hyaena. This might be accounted for by its greater abundance and availability locally. In central Iran, striped hyaenas unintentionally maimed in vehicle collisions or in traps intended to catch problematic wolves are often killed or dissected opportunistically for their organs (Tourani *et al.*, 2012). In Limpopo Province, carcasses of brown hyaenas killed by cars may be removed for use in *muti*. Several respondents from the Thalane community told stories of people bringing the fur of hyaenas killed in road accidents to *sangomas*. In a study sampling roadkill frequency in northern Limpopo, the body of a brown hyaena was found with its tail removed (Collinson, 2013b).

Hyaena tail is a powerful aid for protecting from theft or enabling house breaking, and as a hunting aid. The smoke from burning part of the tail sends residents and prey into a heavy sleep akin to death, which succours illegitimate access or hunting (Collinson, 2013a; Niehaus *et al.*, 2001). In the Thalane community, several people told me about how a witch can light hyaena tail hairs by the door of a house so the smoke possesses the person inside. The witch will command the occupant to open the door for him and the occupant will do so without resistance. Then the occupant will fall into a deep sleep and the witch can steal everything inside, even the bed from underneath a sleeper's body, without being detected. One white Afrikaans landowner told me that he experienced an extensive robbery in his workshop during the night and his eight guard dogs did not bark. The next day the police were called and the policeman said that the thieves must have used a wolf's tail (hyaena's tail) to make the dogs sleep. A mixture created by *sangomas* of hyaena forehead and snake parts is smeared across

the door of a shop or in a car to avert robbery. Using hyaena body parts to either prevent or aid theft links to the scavenging and kleptoparasitism behaviour exhibited by hyaenas. Many of the beliefs I recorded about hyaenas in witchcraft or traditional medicine stem from biological foundations, indicating a link between witchcraft and science. These include scavenging behaviour, nocturnal activity, the long distances hyaena travel nightly, and their refined sense of smell.

A traditional healer told me that she uses brown hyaena hair rolled in a circle and mixes it with medicine to help improve business at people's shops. The hyaena's nose can be used to help relocate lost items; this links to biological attributes. With their acute sense of smell, brown hyaenas can smell old, dried carrion as far as four kilometres away downwind (Mills, 1987). Therefore although many black people nowadays have little knowledge of hyaena behavioural ecology, their traditional beliefs hark back to scientific truths. The *sangoma* also uses hyaena parts to treat people who are mentally ill. Mixing hyaena parts with other medicine is thought to be calming. The tail can also be used to help incarcerated people who were wrongly accused of a crime. Mixing the hyaena tail with lion fat helps a defendant in court to walk free.

One *sangoma* said that the most highly demanded animals for his medicine are hyaenas, elephants, and lions. *Sangomas* acquire hyaena parts from roadkill, people who catch and sell them, and from farmers who shoot them.

In the Thlane community, brown hyaenas are disliked to a much greater extent than amongst the Buys or the commercial farmers. Although this may be attributed to lower education levels and a more widespread perception that brown hyaenas pose a physical danger to people, associations with witchcraft and a strong belief in witchcraft are significant factors. Some members of the Thlane community stated that they like animals, even hyaenas, but they do not like how humans use them for witchcraft, curses, and traditional medicine.

"It's not a bad animal but the people use it for bad things but this animal I don't have a problem." [C11]

They are afraid of these animals, not because of their nature, but because of the evil powers that are imbued in them by people.

Although negative attitudes about animals can stimulate negative actions towards them (Marchini and Macdonald, 2012), in the Thalane community fear of brown hyaenas due to associations with witchcraft may provide the species with some protection. Most members of the Thalane community seldom visit the mountains because they believe that spiritual beings such as Dyambilia and animals associated with witchcraft like brown hyaenas reside there and they are frightened of encountering these animals. The difficult terrain is an additional deterrent, meaning that instances of snaring are less prevalent in the Soutpansberg Mountains than low-lying areas. However, brown hyaenas have large home ranges and mountain-dwelling animals often frequent low-lying areas where snares are abundant (Chapter 6), thus negating some benefits of their montane seclusion.

Perceptions about animals which stem from traditional belief systems may wane in forthcoming years as traditional practices become less ingrained in rural black communities (Afqlayan, 2004). These transitions are already occurring within the Thalane community. Girls within the community used to participate in a ritual to welcome womanhood, which involved spending several days on Thalane hill. This was disbanded in recent years and many of the younger people in the community do not know the traditional stories about animals while their grandparents do. Interpretations of animals are passed down through generations (Arluke and Sanders, 1996, p. 9), yet in the Thalane community the flow of this information seems to be stagnating.

3.4.3. Attitudes towards brown hyaenas

On a five-point Likert scale (strongly dislike to strongly like) (Kaczensky *et al.*, 2004; Muris *et al.*, 2010; St John *et al.*, 2011; Thorn *et al.*, 2011a), interviewees ranked their attitude towards brown and spotted hyaenas (Table 3.4). Some respondents feel neutral towards hyaenas but most have a more extreme attitudinal response. Group A

respondents have an average Likert scale score of 3.82 for brown hyaenas and 3.07 for spotted hyaenas indicating that the average respondent likes hyaenas. Many members of this group did not mind sharing their land with brown hyaenas despite this group's more frequent experiences of and potential for human-hyaena conflict. Their high acceptance level may be attributed a higher level of education overall. Education can improve tolerance to human-wildlife conflict (Holmern *et al.*, 2007; Marker *et al.*, 2003a; Thorn *et al.*, 2011a). Less educated respondents have far more negative perceptions of wolves than people with college educations or those who test high for animal knowledge (Kellert, 1985b). A similar trend of more educated participants holding more positive attitudes towards predators is found amongst community members bordering Kruger National Park (Lagendijk and Gusset, 2008), and respondents in Tanzania, Rwanda, Brazil, and the USA who have less knowledge about wildlife are less supportive of conservation (Harcourt *et al.*, 1986). Education is not necessarily the most important factor driving positive attitudes towards wildlife, as illustrated in Kenya where the uneducated populace also reap benefits from tourism and therefore hold positive attitudes towards elephants (Gadd, 2005).

Table 3.4 Average attitudinal scores towards brown hyaenas in and around the Soutpansberg Mountains in relation to interview group, gender, age, conflict, and education. Likert scale: 1 = strongly dislike, 2 = mildly dislike, 3 = neutral, 4 = mildly like, 5 = strongly like.

		Average Likert score across all groups	Average Likert score group A	Average Likert score group B	Average Likert score group C
Overall		2.87	3.82	2.91	1.59
Gender	Female	2.06	4	2.71	1
	Male	3.23	3.85	3.05	2.24
Age in years	<30	2.28	4.33	3.5	1.5
	30-59	3.15	3.87	3.07	2
	60-90	2.71	3.7	2.63	1
Problems with brown hyaenas	Yes	2.53	2.82	2.2	1
	No	2.91	4.31	3.03	1.66
Years of formal education	0-5	1.47	N/A	1	1.5
	6-10	2.68	2.6	3.3	1.77
	11-15	3.1	3.95	2.46	1.67
	16-21	4.37	4.25	N/A	N/A

Group A respondents understand and appreciate the biological services that scavengers provide. Supposed losses of livestock on cattle ranches or ungulates on game farms attributed to marauding carnivores affects negative attitudes (Lindsey *et al.*, 2005), yet net benefits are more influential in defining attitudes than offsetting wildlife damage (Bauer, 2003; Románach *et al.*, 2011).

The few commercial farmers who said that they did not like brown hyaenas have lower formal education and believe that they are experiencing livestock losses by hyaenas. Direct interaction with animals often creates a positive attitude towards them (Kellert, 1985a) unless conflict is experienced (Dowle and Deane, 2009; Lindsey *et al.*, 2013b). Respondents who live in closest contact with brown bears in Croatia and experience financial losses hold the most negative attitudes toward bears (Majic *et al.*, 2011). Compared to the commercial farmers who learn about nature from first hand experiences and interacting with other farmers, the Buys and Thlane people gain much of their knowledge about wildlife from television programmes rather than the

real world. This biases their knowledge of predators to more iconic and visible animals like lions. Overdramatised media portrayals may have perpetuated associations of predators as frightening killing machines. The majority of people in group B and C dislike brown hyaenas. Group B rank brown hyaenas on average as 2.91 on the Likert scale and group C rank brown hyaenas as 1.59. Brown hyaenas are perceived as a threat to human wellbeing and livestock despite the fact that only three respondents experienced livestock losses from brown hyaenas and no one could recount a case of a brown hyaena attacking a human.

Spotted hyaenas are more hated amongst group A respondents because they are considered a greater threat to livestock and game, but group B and C respondents are more likely to group all hyaenas together and thus almost no attitudinal differentiation is detected between the two species.

Attitudes towards animals are shaped by self-interest, empathy/identification, and beliefs regarding the nature and status of animals (Hills, 1993). Attitude types towards animals can be broken down into several categories (Table 3.5) (Kellert, 1985b).

Table 3.5 Attitudes towards animals and their defining characteristics (Kellert, 1985b).

Category	Defining characteristics
Naturalistic	Primary interest and affection for wildlife and the outdoors.
Ecologistic	Primary concern for the environment as a system, for interrelationships between wildlife species and natural habitats.
Humanistic	Primary interest and strong affection for individual animals, principally pets. Regarding wildlife, focus on large attractive animals with strong anthropomorphic associations.
Moralistic	Primary concern for the right and wrong treatment of animals, with strong opposition to exploitation of and cruelty toward animals.
Scientistic	Primary interest in the physical attributes and biological functioning of animals.
Aesthetic	Primary interest in the artistic and symbolic characteristics of animals.
Utilitarian	Primary concern for the practical and material value of animals.
Dominionistic	Primary satisfactions derived from mastery and control over animals typically in sporting situations.
Negativistic	Primary orientation and avoidance of animals due either to indifference, dislike, or fear.

The attitudinal category people most strongly identify with is dependent upon age, gender, urban/rural surroundings, education, pet ownership, participation in environmental activities, and vocation (Dowle and Deane, 2009; Hills, 1993; Kellert, 1985a; Kellert, 1985b; Kellert and Berry, 1987). A study in the United States determined that gender is the most important demographic factor affecting attitudes, knowledge, and behaviour towards animals. Females express a stronger emotional attachment level to animals and a more humanist and moralistic approach with greater anthropomorphic associations than males (Kellert and Berry, 1987). In the North West Province, South Africa, tolerance towards carnivores is lowest amongst Afrikaans-speaking farmers and older people (Richmond-Coggan, 2014; Thorn *et al.*, 2012). In and around the Soutspanberg Mountains, males are more positive about hyaenas than females with the exception of group A respondents (Table 3.4). This may be due to males' greater experiences with nature. Overall, respondents aged between 30 and 60 are more positive about hyaenas than younger and older respondents yet in groups A and B positive attitude decreases slightly with age. Appreciation of brown hyaenas increases with more education.

Many of the themes indicated in Table 3.5 affected respondents' perceptions towards brown hyaenas. Sometimes several characteristics define attitudes simultaneously similar to the utilitarian-plus relationship described by Knight (2005) where farmers of domestic animals hold a utilitarian and moralistic approach. Some animals which are useful to humans as food (turkey, chicken, trout, lobster) or are useful in other ways such as insects, which maintain soil properties, receive low ratings for intelligence and loveliness while other food animals (sheep and pigs) rate more highly on both fronts (Driscoll, 1995). Relationships with livestock are influenced by multiple attitudinal factors (Evans-Pritchard, 1940; Ferguson, 1985). Interviewees experience brown hyaenas in relation to naturalistic, scientific, aesthetic, utilitarian, dominionistic, and negativistic themes and are often influenced by several concepts simultaneously.

Naturalistic:

Legendijk and Gusset (2008) found that the most important factor influencing human-carnivore coexistence on land bordering Kruger National Park is the belief that

predators are an integral part of nature which has a right to live there and be preserved for future generations. Similarly the Buys' naturalistic approach and belief that wild animals belong regardless of their behaviour meant that they want to preserve wildlife for next generation. They value the native animals and even after an incident of livestock depredation, they will often seek a non-lethal approach. Consequently, the Buys were more likely to contact the government's nature conservation department (informally called Nature Conservation) for support than group A respondents. One Buys male expressed sympathy towards brown hyaenas because humans threaten them and he does not want them to face extinction.

"I would say that I don't like knowing that this animal is busy decreasing, the same with the leopards and all the predators. I would like it if they were always here. And if it is really a problem there must be other ways to deal with them, that's how I feel about any predator, the lion and everything. They can become a problem I don't argue with that but humans are the invaders here." [B09]

Scientific:

The brown hyaena's scavenging behaviour is sometimes perceived as a negative attribute, which symbolises cowardice, sneakiness, and weakness by group B and C interviewees. However, when shown a photo of a lion, respondents employed honourable monikers such as 'Uncle Leo', 'king of the beasts', 'the big boss', and 'the king of the mountains'. Admiration for the lion is due to its prowess as a hunter and indicates the importance of cultural perceptions in defining attitudes. Similar admiration towards lions is found in the Maasai culture (Goldman *et al.*, 2010).

Aesthetic:

Opinions of animals are often based on visual perceptions rather than knowledge of the animal's behaviour (Smith *et al.*, 2010). Structural and visual interpretations are one of the strongest determinants of attitude in and around the Soutpansberg Mountains.

Many opinions about brown hyaenas are based upon their unusual physical appearance. As a mostly 'invisible' animal, some people may have only glimpsed the hyaena's long mane and sloping back silhouetted in the dark, which can appear very frightening. As many interviewees have never seen a hyaena, it felt like they tried to gather as much information as possible from the photograph I provided. Across the groups, quite a few people said they did not like hyaenas because they are ugly or look scary, or alternatively some people liked them because they are beautiful or fluffy. Positive visual descriptions are often coupled with labelling the animal as dangerous which affects an informant's composite attitude.

Aesthetics are especially important to the Buys people not only in terms of their opinions towards animals but also regarding the landscape. Many people are proud of living in Buysdorp because of the beauty of the mountains. By keeping the mountains beautiful, they are preserving the landscape that greeted Coenraad du Buys when he first came to the Soutpansberg Mountains in the early 1800s. Unlike the Thlane, the Buys do not overharvest the trees in the mountains. Each household placed at the base of the mountain has stewardship of the area behind their home and takes pride in keeping it pristine. Natural beauty is linked to a sense of peace, quiet, and calmness, which many people appreciate. Wild animals are an intrinsic component of the mountain's natural beauty, although sometimes predators are considered to taint the peacefulness.

Religion also has an effect on how people viewed animals. Cosmological identification can invoke conservation-mindedness based around 'cosmic purpose ethics' (Fox, 1990, p. 175). For many Buys people, animals are appreciated because God created them and gave each animal a purpose. Some people expressed negative opinions about hyaenas but still like them because God created them.

Utilitarian:

Perceptions about brown hyaenas, both negative and positive, are often based around utilitarian concepts. Overall, brown hyaenas are not perceived to be very useful animals and this impacts on their popularity. Nevertheless, the brown hyaena's

‘uselessness’ combined with its ‘invisibility’ protects it from persecution by group C respondents.

A large proportion of people from the Thalane community do not like hyaenas because they cannot eat them; consequently they are perceived to be valueless. Many people in the community expressed that if an animal could not be eaten or used, then it should be removed. In the Thalane community, several people eat predators such as jackals, caracals, or servals, especially if a fresh carcass is found as roadkill. Brown hyaena, however, is considered inconsumable.

“I hate them (brown hyaenas). I hate them...Because of the problems they give and I never see the benefit because I can’t even eat them even if I want to shoot them.” [C08]

A similar trend of eating mesopredators but avoiding hyaena consumption was observed in Malawi by Morris (2000b). A few respondents commented that brown hyaena skins could be used for clothing in rituals or ceremonies. Brown hyaena body parts are important for *muti* but there is limited demand. The Thalane’s strongly pragmatic point of view aligns with their opinion of nature in general. Rather than appreciating the mountains for its beauty or calmness like the Buys do, the Thalane appreciate it for the useful functions it provide such as blocking the wind and rain. A utilitarian approach towards animals is more prevalent in lower income communities due to the urgency to meet basic needs (Infield, 1988). Aesthetic or naturalistic approaches are more accessible after basic needs have been met.

Group A respondents also consider the brown hyaena from a utilitarian point of view, but in regards to income generation or loss rather than basic needs. Financial gain is a big driver behind how group A respondents view wildlife. If a hyaena kills livestock and reduces potential income generation then it oversteps the line of acceptability and should be removed. Conversely, brown hyaenas produce income for some trophy hunting outfitters through organised hunts. One interviewee stated that he could earn 25,000 South African Rands from a brown hyaena hunt and as a result he would like many more brown hyaenas on his land.

Domionistic:

Most hunting farms said that their clients express little interest in hunting brown hyaenas. Hyaenas are unpopular trophies due to their ungainly appearance, status as pests, and the lack of danger in hunting them that 'big five' animals present (Johnson *et al.*, 2010; Mills and Hofer, 1998). Additionally, a government permit is required to hunt brown hyaenas (Department of Environmental Affairs and Tourism, 2007), which dissuades some game farmers. One game farmer, however, said that there is a high demand for brown hyaena hunts by his mostly eastern European clientele. Some international hunters come to Africa to collect as many different species as possible (Johnson *et al.*, 2010) and these hunters are interested in the brown hyaena because it is a rare and unusual piece for their collection.

Negativistic:

Fear of animals due to perceptions of harm can significantly influence attitude (Kaczensky *et al.*, 2004). Attitudes towards brown bears in Slovenia could be predicted based on how harmful people perceived bears to be (Kaczensky *et al.*, 2004). In Buysdorp and the Thalane communities, a lot of people believe brown hyaenas eat people and this accounted for some negative attitudes.

"First they (brown hyaenas) are going to eat my animals and then they are going to eat me." [B29]

A song that is taught to Buys and Thalane children in Buysdorp's primary school goes like this *"Children, children, come home. No mama, we can't, the hyaena it's in the way. How big is it? So big. What does it drink? It drinks a person's blood. What does it eat? It eats people."* The person pretending to be the mother calls the children, the children scream, and the child pretending to be the hyaena chases the children. Fear of hyaenas is also closely linked to associations with witchcraft.

The Buys and Thalane people view the less fearful relationship that white people have with predators with suspicion.

“You white people you kiss this stuff (predators), you are not scared, what if the hairs go into your mouth, no, I don’t know.” [B06]

3.5. Summary

In agreement with comparable studies (Schiess-Meier *et al.*, 2007; Thorn *et al.*, 2013), human-brown hyaena conflict is generally quite low compared to other large predators. The prevalence of more destructive predators adds to the brown hyaena’s invisibility, buffering the species from some negativity and retaliatory behaviour. Commercial landowners’ tolerance towards the species is high as long as hyaenas adhere to human standards of acceptable behaviour. Variation in what is considered acceptable creates a confusing landscape for hyaenas to function safely in. Despite a relatively low level of reported persecution in response to perceived or real depredation, the brown hyaena population is also threatened by snaring and road traffic accidents.

Although some commercial farmers view the hyaena’s invisibility positively, its elusiveness reinforces links to witchcraft and the occult. Many people in the Thlane community fear brown hyaenas because of these connections and misconceptions about hyaena behaviour, especially in relation to man-eating.

Attitudes towards brown hyaenas are created from direct experience, cultural constructs, utilitarian benefits, and other factors. Often several competing factors influence how people perceive brown hyaenas. Group A experiences the highest level of conflict with predators, yet they are the most accepting. One of the most influential factors is their higher level of education. The opposite trend of dislike towards and fear of hyaenas is found with group C respondents who have the lowest level of education.

Conservation initiatives should make the ‘real’ brown hyaena more visible for rural African communities whilst considering indigenous knowledge systems (Gadgil *et al.*,

1993; Kideghesho, 2009). Although the brown hyaena may have been protected from retaliatory behaviour due to its invisibility, some commercial farmers also need to see the 'real' animal and appreciate the biological benefits they supply.

Public support for conservation frequently depends on the attractiveness of the animal species in question. It is easier to gain public support for attractive animals with anthropomorphic potential such as giant pandas (*Ailuropoda melanoleuca*) or sea otters (*Enhydra lutris*) than insects, reptiles, or fish, even if the less charismatic species is highly endangered (Driscoll, 1995; Kellert, 1985b; Sitas *et al.*, 2009; Smith *et al.*, 2010). The hyaena's appearance disadvantages it on the conservation agenda, yet through positive portrayals such as promoting their ecological roles and dispelling associations with livestock killing, it will hopefully in time be seen as an animal worth protecting.

Chapter 4: Power structures and human-brown hyaena relationships

4.1. Introduction

Human-predator conflict can disguise complex conflicts between groups of people (Dickman, 2010; Madden and McQuinn, 2014). Hidden human-human conflicts are often overlooked in approaches to mitigate human-wildlife conflict (Madden and McQuinn, 2014). In addition, the relationships between people and predators differ across socio-economic groups for a multitude of reasons (Romañach *et al.*, 2007; Williams, 2011) including historical legacies from periods of political inequality (Rust *et al.*, 2016) and other social factors (Dickman, 2010).

In this chapter, I examine how the power of the meanings people attach to predators influences human-brown hyaena relations. I investigate how people from different socio-economic groups assume power over nature, and how historical disparities in access to power impact human-brown hyaena relationships in a postcolonial landscape.

4.1.1. Historic power struggles and effects on wildlife management: a case study from Namibia

Periods of extreme inequality and oppression in human history resulting from wars or strongly ideological political regimes have direct and indirect consequences on wildlife (Dudley *et al.*, 2002).

Colonialism and the apartheid regime attempted to justify the denial of rights to specific groups of people through psychological, racial, and imperialist separation of peoples (Donnelly, 2013) (refer to section 2.6 for a detailed description). Although at the end of the apartheid South Africa focused on reinventing itself as a nation with equal human rights for all (Donnelly, 2013), imperialist mentalities can be slow to

reverse, even years after regimes have lifted. Although there are some exceptions (cf. Yufanyi Movuh, 2012 for Cameroon), very little research has been conducted on how psychological programming indirectly affects relationships with wildlife in subsequent years (Rust *et al.*, 2016).

Only one study has investigated how present day social, political, and economic effects stemming from the apartheid era drive human-wildlife conflict in southern Africa (Rust *et al.*, 2016). Rust *et al.* (2016) found that unequal access to resources following the apartheid period creates a perpetuating and interlinking chain of inequalities which provokes human-wildlife conflict in Namibia (Figure 4.1). Like many countries in southern Africa, Namibia has struggled to shake extreme socio-economic divisions between the wealthiest and the poorest members of society (Central Intelligence Agency, 2013). High unemployment and low education levels after apartheid created a labour surplus, which enabled wealthier landowners to pay low wages to their farm workers (Rust *et al.*, 2016). Some landowners who have not shaken racist mentalities established or reinforced during apartheid treat their workers poorly. Farms where workers do not feel valued or experience poor living and working conditions have higher levels of carnivore conflict. This may be because vengeful or unmotivated workers do not enforce anti-predation measures, are involved in poaching of prey species, or steal livestock and blame their disappearance on predators (Rust *et al.*, 2016). Lower prey availability from poaching adversely impacts predator populations and livestock theft provokes lethal retaliation on predators pegged as scapegoats (Rust *et al.*, 2016).

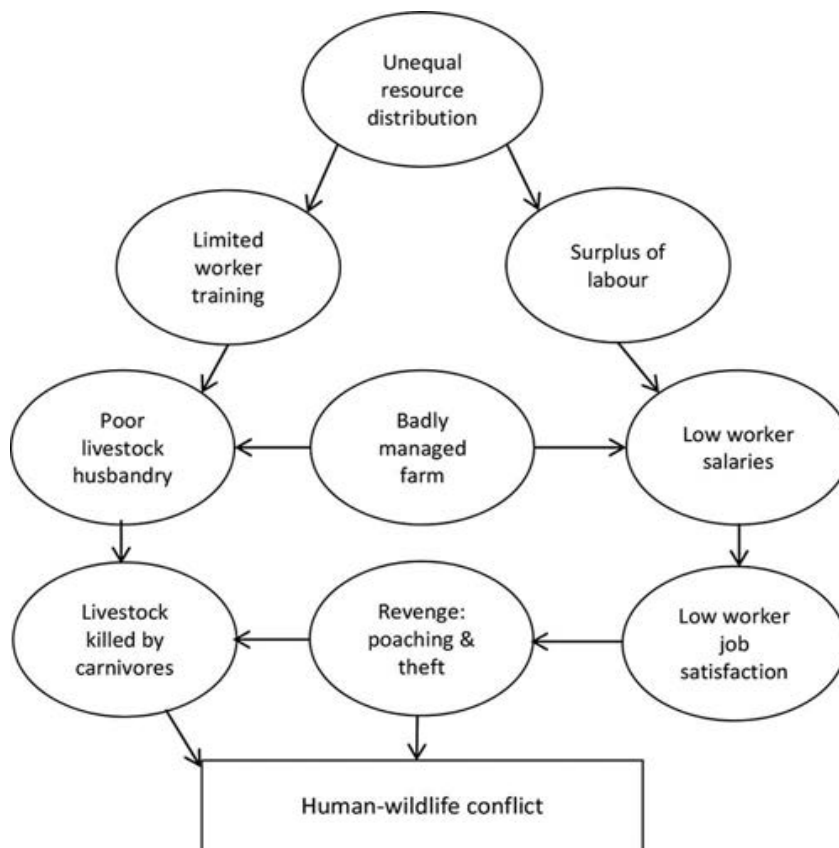


Figure 4.1 Flow chart from Rust *et al.*, 2016 showing the social, political, and economic drivers of human-wildlife conflict on commercial farms in Namibia.

In the Namibian case study, both carnivores and certain groups of people are subjugated at the 'other' through a process of domination (Rust and Taylor, 2016). Plumwood (2003) describes seven stages towards domination in the 'othering' of non-human species. This process is likened to an appropriative colonisation of nature (Plumwood, 2003). These stages are applied by Rust and Taylor (2016) to the Namibian context. By providing examples of how predators and indigenous people were historically and are continually dominated across the seven stages, clear parallels are presented between animal experiences and the exclusionary practices of the apartheid and the colonial era (Rust and Taylor, 2016).

Rust *et al.* (2016) and Rust and Taylor (2016) initiated the first dialogues about how legacies of apartheid delay the resolution of human-wildlife conflict in southern Africa. This chapter aims to expand upon this theme of historic power struggles and predator relationships by exploring how interactions between people and predators mirror a colonial power struggle between colonists, the land, and native people.

4.1.2. Control of land and wildlife by different groups

In southern Africa, ownership of and access to land and its associated wildlife resources is often polarised between groups with greater economic and social power and those with less power (Aliber, 2003; Murombedzi, 2003). Despite South Africa's efforts to employ a land reform and redistribution programme to readdress an ownership bias created during and prior to apartheid (Murombedzi, 2003), the majority of South Africa's total land area is still owned by a minority group of mostly white private farmers (Walker and Dubb, 2012). Consequently, relationships with wildlife remain embedded in deeper issues relating to historic power structures.

Power over land and legal control of wildlife by white people is embedded in cultural and personal identities. Working the land has been idealised in the Afrikaans mind through novels about farm life called *plaasromans*, songs, and poetry (Huggan and Tiffin, 2010). The traditional image of a strong and devoted Afrikaner is of a man who can control the bush and be economically successful doing so (February, 1991). Farm ownership and management is often romanticised and considered a sign of masculinity, power, wealth, and entitlement (Huggan and Tiffin, 2010). In the Soutpansberg Mountains, land ownership and management is an essential component of the Afrikaans identity and symbolises achievement against environmental, economic, and social challenges (Fraser, 2008). Farming's symbolic importance influenced some Afrikaners' refusals to sell their farms to the government (Fraser, 2008). Even white South Africans who reside in urban centres often express nostalgia for the bush, as demonstrated by the popularity of owning game farms as a retreat, holidaying to game reserves, and partaking in recreational activities like hunting (Du Pisani, 2001).

Successful farm management involves defending the land from people or animals that may jeopardise a farmer's control and productivity. It invokes pride and is a testament to the multi-faceted struggles of the heroically presented voortrekker settlers and previous generations of family members who cultivated the land (Fraser, 2008; Goodrich, 2013). When a white farmer's control over his land becomes threatened, whether this is by predators, poachers, or a land claim, the impact is felt deeply

because it not only endangers the farmer's economic stability, but also threatens the farmer's perceptions of his personal and cultural validity (Goodrich, 2013).

Control over land and wildlife by black people in northern Limpopo is largely limited to smaller tracts of communal land adjacent to townships (Constant *et al.*, 2015). These areas are primarily used for subsistence farming, and animals such as cows, goats, and donkeys are kept for meat, milk, labour, and cultural purposes (Constant *et al.*, 2015; Shackleton *et al.*, 2000). Multiple members within the community claim joint ownership of these areas, natural resources, and livestock. Communal land often lacks permanent fences (Constant *et al.*, 2015); this in itself symbolises reduced absolute control compared to white-owned private properties. A more laissez-faire mentality regarding management of the land and animals is prevalent (Constant *et al.*, 2015), partially because of communal ownership (Hardin, 1968) and partially because control over land does not have the same personal importance and historical meaning as it does for white farmers. Despite a more relaxed management approach, depredation of livestock has serious implications for communal farmers. People in communal areas often have low economic resources and therefore higher vulnerability to losses of livestock by predators (Constant *et al.*, 2015; Holmern *et al.*, 2007; Wang and Macdonald, 2006). People with greater economic instability are more likely to kill carnivores (Mattson, 2004). Due to the cultural importance of livestock, losses can also have hidden spiritual repercussions (Constant *et al.*, 2015).

Communal and private land management represent legal approaches to asserting control over land and animals. Illegal elicitation of control over wildlife such as through poaching is often associated with unemployment and lower economic status (Lindsey *et al.*, 2011a). These actions are more secretive yet their impact can be extremely powerful, not only on predators but also on other humans who may feel violated at an intrusion on their private property (Gombay, 2014).

In addition to the human position, I examine the intricate power that predators' presence and actions have over people. Although large predators are regarded as powerful, both physically and culturally (Kruuk, 2002), they are essentially voiceless

(Freeman *et al.*, 2011), therefore they can become pawns in what is fundamentally human-human conflict (Dickman, 2010).

4.2. Methods

Methods and data analysis techniques are described in Chapter 3. An introduction to the three main socio-economic interviewee groups (Group A: owners and managers of private land/nature reserves, Group B: coloured members of the Buysdorp community, referred to as the Buys, Group C: black members of the Buysdorp community, referred to as the Thalané) is provided in section 3.3.4.

4.3. Fieldwork reflections

4.3.1. Powerful predators: controlling humans

In and around the Soutpansberg Mountains, farming is frequently, but not exclusively, perceived as a constant battle to control nature. The presence of large predators is identified as one of the biggest challenges in this pursuit because these animals are difficult to regulate and can cause high levels of damage on large and valuable game species and livestock. Insect pests such as ticks can also inflict huge detrimental effects on wild and domestic animals (Pfäffle *et al.*, 2013), yet their presence is subtler and the damage they wreak is frequently slower and less obtrusive. Insects, which are difficult to identify with and ascribe human characteristics to (Driscoll, 1995), are often held less responsible for damage than predators. Commonalities between humans and predators are more easily found because of shared traits as mammals and as animals that dominate the landscape they inhabit (Horowitz and Bekoff, 2007; Hurn, 2012). Consequently, damage by predators can be perceived as deliberate, malicious, or cruel (Woodroffe and Ginsberg, 1999). Predators can creep undetected in and out of farms but once inside, their powerful teeth and claws leave obvious bloody wounds upon their prey, creating a frightening image of an animal that is simultaneously stealthy and bold.

The fear of predators that many people have is largely connected to the multi-faceted power they have over people (Arluke and Sanders, 1996). As a predator, the brown hyaena is considered distinctive from non-predatory species due to symbolic properties. Some people are afraid of hyaenas because they are wild animals and therefore considered untrustworthy and difficult, yet not impossible, to control. One respondent summed up this sentiment, *“A wild animal stays wild.”* [B06].

Respondents in group A and B compared predators on their land to thieves breaking into a house.

“I wouldn’t really care much but you know it’s always painful if you lose something. You know who is the cause of it. It’s like a thief coming to steal or break into your house you know. If you know who it is, you won’t like that person.” [B11]

This commonly recited metaphor demonstrates the control that people perceive predators to have, and the vulnerability and helplessness farmers feel. Predators are seen as having the potential to control every aspect of a farmer’s life - economically, socially, mentally, emotionally, and culturally.

By killing livestock or expensive game, predators deny farmers’ financial control. Through depredation or death from another cause that is incorrectly attributed to depredation, the farmer loses the cost of the cow (the average cost of a weaned calf is 4,000 South African Rands) or the game animal. One respondent shared a story about his neighbour who bought a sable antelope calf for 250,000 South African Rands, only to have it killed by a leopard shortly after purchase. Not only does the farmer lose the animal’s purchase or selling value but also the future breeding potential of the predated individual. Group C respondents report that the loss of a cow or goat has additional cultural repercussions. These animals still have value for bridewealth, funerals, and status. For example, in the Venda culture, the *makulu* (a messenger to the ancestors) goat is used to communicate with the ancestors and ask favours. However, in recent years the cultural value of livestock has diminished significantly within the Venda and Sesotho communities who more commonly pay the *lobola* (bride

price) with money and show status through material possessions such as cars and electronics.

Losses incurred by predators have detrimental impacts beyond the financial realm. One farmer said he feels like he cannot leave his property to go on holiday because he must kraal his livestock daily in order to protect them from predators. He cannot afford any losses financially and feels like he had no other option but to stay bound to the land. He spoke about his situation as if he is a slave to the predators and this lack of freedom clearly upset him.

How a farmer responds to problems with predators influences how they are perceived by their peers. Some farmers expressed that if they respond to depredation by killing the animal believed to be responsible or alternatively let the animal live, they will be judged by other farmers and members of the wider society. The illegal act of killing large predators transforms the farmer into a criminal, which may not be a label a farmer wants to be known by. Possible persecution and judgment leads many farmers to keep quiet about retaliatory killings. Despite reluctance by some farmers to participate in lethal retaliation, many farmers feel this is only solution to their predation problem due to poor governmental support or lack of resources, therefore ironically, by killing a predator they become a 'slave' to predators.

The burden of being rendered financially and holistically vulnerable by predators makes some interviewees feel stressed, distraught, and hopeless.

"You know if the leopard would just, if just concentrated on impala or whatever, they could have one a week as far as I'm concerned. It wouldn't bother me at all. But why must they take my calves?" [A36]

One farmer deliberately did not keep records of predation events because he did not want to be discouraged from farming.

Although the brown hyaena is not believed to be a livestock killer by the majority of respondents who own or manage private farmland, brown hyaenas are still viewed as

untrustworthy because of their status as a predator and a possible threat. Therefore, despite provoking substantially less conflict than leopards, hyaenas are still perceived as a powerful animal to be wary of.

4.3.1.1. Brown hyaenas as powerful animals

Almost one third of respondents refer to the brown hyaena as a powerful animal. Its dominant status invokes fear, but also respect, similar to perceptions of lions in Kenya (Goldman *et al.*, 2010). The brown hyaena's power is attributed to its identity as a predator, its physical toughness (mostly by group A and B respondents), and its association with witchcraft (group C).

Several people explain how tough brown hyaenas are and how difficult they are to kill. One farm manager shared a story about trying to kill a brown hyaena that was threatening their nyalas.

"We went out and we shot him (the brown hyaena) but it took six shots and after three shots in the head we put the silencer in his mouth and he bit that silencer with three shots in his head. So the sixth shot in his head at point blank range killed him so they don't die for nothing those things. And it was extremely ugly, they are nice from far but close up they are ugly things. I saw the strength in that thing, to bite through a silencer is not easy and after three shots in the head and it wasn't like it was just nerves or something, it was still alive because it was still trying to get up." [A14]

On several occasions, respondents mentioned the hyaena's powerful jaw when discussing the animal's physical strength. Farmers gave examples of brown hyaenas biting through fences, electric lines, steel wires, bottles, and bones, as exemplified in this quote:

"But sometimes the neighbour's hyaenas will bite a hole in the fence from outside which isn't electrified and they come in. But it's not a desirable animal

to have there, they walk and chew, they can chew through pieces of steel.”

[A16]

Additionally, the brown hyaenas' power is regaled in stories of its dominance over leopards, either by stealing baits which are set for leopard trophy hunts or by thieving food from leopards on game farms, causing the leopard to kill again 'unnaturally' soon. Examples of brown hyaenas dominating other animals are used as an analogy for the brown hyaenas perceived control over people and the wider landscape.

Predators are not only powerful from a physical point of view, but also in terms of the magic they provide witches and *sangomas* (section 3.4.2). This is especially true for hyaenas; they are considered the most powerful animals for witches as important ingredients in *muti* (section 3.4.2) and as familiars. Several local *sangomas* indicated that the brown hyaena is more powerful than the spotted hyaena. This is surprising considering the brown hyaena is a less successful hunter and is smaller in size than the spotted hyaena (Mills, 1984). Yet the brown hyaena is more locally available than the spotted hyaena and their comparative abundance may explain their elevated status. Black informants also discussed the brown hyaena's ability to survive in difficult situations, yet they perceive the hyaena's strength as stemming from its magical properties rather than its physical prowess. One *sangoma* said that during the day when the brown hyaenas are sleeping, they start walking at night in their minds so people cannot catch brown hyaenas with snares because they dream where to walk safely in advance.

4.3.1.2. Brown hyaenas crossing into human boundaries

A common theme amongst some group A and group C respondents is that there are spaces that are acceptable and unacceptable for brown hyaenas to enter. Informants assume a high level of insight on the brown hyaena's part; for example some respondents suggest that hyaenas should know to avoid farms where they are not welcome and areas of high human habitation. They should stay in the mountains or the nature reserves where they 'belong'. A similar spatial expectation exists for

leopards that cross from Blouberg Nature Reserve (where they belong) to neighbouring communities (where they do not belong) (Constant and Bell, in press). This ideology is in line with the concept expressed in Chapter 3 that brown hyaenas are acceptable as long as they do not bother the interviewee. As soon as a hyaena enters a non-acceptable part of the human landscape, the animal becomes an intruder by taking control from the landowner and transforms from a neutral being into a problem animal. A hyaena intruding in certain human landscapes evokes negative stereotypes of hyaenas as thieves.

This concept is applied to other potentially dangerous animals as well. Snakes are accepted in the bush but when they cross an invisible radius around a homestead they are considered a problem, which must be addressed.

It is challenging to define the areas that brown hyaenas are allowed to move because the invisible lines of acceptable predator presence differ between respondents. Some people expressed that there are designated places for predators such as national parks and zoos and that they should only exist there. This cohort of respondents argue that farmers should not feel guilty about discouraging predators on their farms because these animals should go to Kruger National Park where they are welcome.

“They (brown hyaenas) must go there, they must live there in Kruger Park or somewhere, not here. Or Indermark... There’s places for those animals, that’s how I feel. I don’t want it here because I’m not into, how can I say, predator animals so we don’t want that. There is places for them and let them be there and that’s fine. If it’s a reserve or something fine. But we are farming here with animals that is tame like the cattle and that and they don’t have a chance against animals like that so we don’t want it here.” [A37]

Expecting all the brown hyaenas to shift to nature reserves seems naïve in regards to the animals’ biological needs and spatial abilities. It also implies that hyaenas recognise the problems their presence presents and that humans dictate where species can exist. Many group B respondents provide an alternative opinion. For the Buys people, there seems to be a division between the wild world of the mountains

and the civilised flatlands where they live. Mountains and surrounding areas are often classified into human spaces and animal spaces and thus can be of benefit to carnivore conservation because through this mind-set, mountains become void of human impact (Mattson, 2004). In Buysdorp, the mountains present a more visible line dividing human and animal areas than the more ambiguous and individually defined human-animal boundaries perceived by group A respondents. The Buys men mainly hunt kudu, impala, bushpig (*Potamochoerus larvatus*), and warthog in the flatlands (the human space) rather than in the mountains (the animals' space). The species they hunt are considered accessible for humans and despite being wild they fall into a different category than the animals considered truly wild and potentially dangerous which live in the mountains.

Sensitivity towards trespassing on private or communal land by predators is compounded by human-driven forces, which also violate ownership and induce vulnerability, such as the land reform process or snaring. Several farmers said the biggest problem and threat to their livestock is the 'two legged predators' or human poachers. One group A landowner said that during apartheid the police looked for snares and caught poachers, but now this no longer happens and no one cares about addressing snaring.

4.3.2. Powerful people: control and ownership over wildlife and land

Regardless of the complex power structures attached to predators, some respondents stated that man is the most powerful predator in the area. This view is most common amongst the Buys people (group B). Several respondents indicated that at a species level, humans are the most formidable contender due to a natural hierarchy. This belief hinges on a clear distinction between human and non-human animals, yet this distinction can be difficult to define (Sax, 2007). Suggested disparities include the lack of verbal communication, intentionality, symbolising, emotional response, soul, autonomy, and consciousness in animals (Arluke and Sanders, 1996; Berger, 2007; Elder *et al.*, 1998; Ingold, 1988; Regan, 2007). With no universally accepted definition of what is human and what is animal, studies of human-animal relations must

consequently draw upon a myriad of socio-ecological ideas. One recurring ideal is anthropocentrism or the belief that human beings are more important than other animal species (Ritvo, 1995). This belief is closely linked with Christianity. The Bible states that God bestowed authority over all other beings to humans, who were created in his likeness (*Genesis*, 1:26) (Cassidy, 2001; Ritvo, 1995; Shanklin, 1985). Strong Christian values present amongst many interviewees shape their beliefs in human superiority. One respondent from Buysdorp stated that humans are intellectually superior to animals because they can think, reason, and have a free will. He was very clear that humans belong in a separate category to animals. According to him, *“Animals are designed only to survive while humans can design and improve and create.”* [B10]. If one accepts this statement as true, then large predators can be considered extremely adept survivalists when compared to other species lower on the food chain and thus the closest competitors to humans. Defining differences between humans and animals, as listed previously, are often presented as a catalogue of the inabilities of animals rather than their abilities, another way of elevating the human status and endowing humans with power.

The power humans have over animals is a theme ingrained in many interviews. Control over wildlife is largely in the hands of the minority of mostly white people of European descent because they have the greatest access to land, wealth, and education. Group A respondents experience conflict with predators most frequently, yet they are also the group that could reciprocate by displaying the most control over wildlife and its management, mainly because of the large areas they owned. Several group A and B respondents spoke about how the black population does not manage land with the aim to preserve it for the future. They spoke about how black communities are often devoid of trees, native plants, or wild animals, alluding to an inability to provide decent stewardship for nature. Group A respondents felt that their control over land and wildlife through cattle farming, game farming, and hunting is vital to preserve land in a natural or semi-natural state, echoing a form of eco-colonialism (Crowe and Shryer, 1995).

Perceived control over wildlife has a substantial influence on human-brown hyaena relationships. While conducting interviews and participant observation, I encountered

an abundance of taxidermy brown hyaenas and almost all mounts were presented in fearsome poses with teeth bared and crazed eyes (Figure 4.2). This is a common portrayal for predator species (Milgrom, 2010). When displayed, the mount tells an epic story of people verses nature, with people as the victors over a mighty and fearsome carnivore (Patchett, 2008). How a trophy is mounted is a way for a hunter to reflect the version of the animal or of himself that he or she wants others to see (Haraway, 1989; Milgrom, 2010).



Figure 4.2 Taxidermy mount of a brown hyaena at a lodge in Baltimore, Limpopo Province.

To re-establish control after a predation event, interviewed farmers will either kill predators in retaliation or make efforts to sustainably live with predators. Some farmers feel like they must ‘conquer’ invading predators in response to their predation problems. This pragmatic and domineering approach is reminiscent of the conquering of land, people, and resources in colonial Africa.

“If it’s a hyaena then you just sort it out. Hyaena’s easy, it’s a bone eater so you take the marrow bone of a kudu, you put poison inside and he’s the only guy that can take that poison out, nobody else. So you put some bone marrows

there and you know that the only thing that will come and take it is a hyaena and he will come and eat.” [A21]

Lethal responses such as the approach explained above, often offer a short-term solution (McManus *et al.*, 2015), solving the problem temporarily until another predator claims the vacant home range through the ‘vacuum effect’ (Balme *et al.*, 2010; Loveridge *et al.*, 2007; Marker, 2002). Therefore, unless responses to predation events include sustainable approaches, demonstrations of power by farmers and predators could seesaw backwards and forwards indefinitely.

Some farmers conduct preventative management such as kraaling livestock or using livestock-guarding dogs to reduce losses from brown hyaenas and other predators. These farmers feel like they achieved some control over nature in order to protect their domestic or game animals through harmonious means, and are extremely proud of their sustainable management approaches. One such farmer expressed a less domineering mentality towards land management:

“If you are going to farm in the area where they (predators) are, you have got to accommodate them. You can’t farm against them.” [A10]

Farmers who practice non-lethal predator control view their approaches as logical and necessary.

“If you keep them (cattle) in the kraal when they are small you won’t lose anything. When my father was the owner, he was the owner of this land and another property, he was having about 2,500 hectares and.... he farmed with 500 cows, and out of that he lost 20 calves a year because he didn’t put them in a kraal.” [A07]

As well as asserting control over predators, landowners strive to control their land against other environmental, economic, and social threats such as drought and political insecurity. While spending time in farming communities, I gained the impression that farming in northern Limpopo Province is an uphill and continual battle

for survival. Many farmers adopt a survivalist approach, which embodies an every man for himself attitude, whereby farmers manage their property like a small sovereign kingdom. This ‘pioneer mentality’ of fighting against nature has been observed in the Afrikaans community in the western Soutpansberg Mountains previously (Chase Grey, 2011) and a comparison between managing commercial farms and ruling private kingdoms was also made in Namibia (Rust *et al.*, 2016).

Fences surround almost all commercial farm boundaries to demarcate ownership, and to protect farms and animals from disease, theft, and human-animal conflict (Boone and Hobbs, 2004; Kesch *et al.*, 2013; Taylor and Martin, 1987). Although there are no recent estimates (Beck, 2010), in 2000 there was an estimated over 90,000 km of game fencing in South Africa (Falkena and van Hoven, 2000). With fences encircling almost every game farm in the approximately 3.6 million hectares devoted to game farming in Limpopo Province (van der Waal and Dekker, 2000), these fences act as a physical and mental reminder of the independence of farmers who often manage their land like ‘kingdoms’.

The personal survivalist approach developed partially because of a general lack of confidence in government assistance to help landowners as illustrated in this quote:

“They (Nature Conservation) are pointless to contact.... You don’t call them, you keep it quiet, you keep it to yourself, when you find it (a predator), you get rid of it, and that’s it.” [A37]

The survivalist approach is also associated with a strong sense of historical belonging to their land. Several group A respondents expressed that their land has been in their families for almost one hundred years and was passed down to them through the generations. Landowners with a legacy expressed pride in knowing that their family has been tough enough to survive the challenges of farming for generations. A 77 year old farmer, like many group A respondents with a family legacy, wanted to tell his family’s story:

"I am born in this bushveld. Here where the t-junction is, the farm right across that was my grandfather's farm with the name 'Suurbuld'. And my dad lived about 30 km further west and there he was married to my mother and I arrived in the bushes, there wasn't a place where they could take my mother so they went to a lady to help with the birth process." [A19]

4.3.2.1. Knowledge is power

I found that knowledge or perceived knowledge of animals equates to having power over them. Respondents who know the most about predators (primarily group A) are the least scared of them. Group A respondents consequently believe that they could assume control over predators and the environment. Even if some of their knowledge about animals is incorrect, their confidence in the validity of their knowledge affects their actions and attitudes.

Game farmers and managers acquire their knowledge of the bush and wild animals through formal education, and from interactions with family and friends, but also through spending copious amounts of time in the veld and leading hunts. I attended a biltong hunt (for meat) on a game farm. I was impressed at how in tune with nature the professional hunter was as she used tracks, signs, and wind direction to stalk impala. This keen attention to detail transforms people involved in the hunting or game farming industry into modern-day bushmen. The professional hunter exhibited pride in knowing how to track quarry and read the bush.

Group B interviewees have a medium level of formal education compared to group A and group C. Many of them spent time in nature as children but are no longer actively engaged. Therefore their knowledge of nature is intermediate between groups A and C.

Group C respondents have the lowest level of knowledge about animals, partially due to less wealth, less formal education, and less private land ownership. Although indigenous knowledge of nature is still abundant, it is largely confined to the older

generations and within the Thlane community there is little indication that this information is being passed to younger generations. Consequently, group C respondents are more wary of predators and lack confidence in their ability to defend their domestic animals from predation events. Their fearfulness is also attributed to beliefs linking predators and witchcraft.

4.3.2.2. Killing for the sake of killing: masculinity and non-retaliatory lethal actions

In and around the Soutpansberg Mountains, people kill brown hyaenas legally and illegally for specific socio-economic reasons such as trophy hunting or in retaliation for perceived or real livestock losses, and inadvertently through snaring and poisoning. Similar to other large predators, brown hyaenas are also killed to facilitate cultural components of the hunting experience (Hazzah *et al.*, 2009; Marchini and Macdonald, 2012). Goodrich (2013, p. 28) determined that many Afrikaans men hunt “to acquire meat through embodied practice that enfolded within itself a sense of masculinity deriving from a mythic past, and that was a central part of a reciprocal relationship they had with the hunted animal and the land it occupied...”. I detected a similar hunting rationale amongst group A respondents who perpetuate colonial identities. Additionally, hunting is described by some group A respondents as a way to connect with the bush and friends first and foremost, with the killing of animal as only a secondary outcome.

“It’s also a culture, these okes (people) just like to shoot shit. And obviously in the past they used to shoot the impala and the warthogs and stuff, but now it’s got a value and they rather wait for a paying hunter to come so now there’s baboon, monkey, jackal and stuff so they are I must say innocent targets.”
[A16]

“Farmers are a specimen of their own, totally different to rest of human beings. If they see an animal, they shoot them on sight. This goes for leopard, caracal, brown hyaena, jackals. My son-in-law is a farmer in the Free State and he kills

jackals. I try to convince him but he keeps going, taking more and more. They don't see reason." [A11]

Some farmers indicate that they killed non-valued wildlife such as brown hyaenas for personal enjoyment, to exercise their ability to hunt, or to mark their dominance over their land. One farmer who did not have a big problem with brown hyaenas still killed them or persecuted them, partially for enjoyment. The following quote expresses his macho sentiments associated these behaviours:

"A month ago we find one (a brown hyaena) and we were chasing it with the bakkie (a truck) and shooting at it. It was big fun. You can't hit it with a bakkie running. It was big fun. We always joke about and say every time a bullet goes off he goes one gear down and then speed up and speed up." [A21]

Machismo is rife within many group A respondents. Many of these interviewees are involved in a hunting culture where bragging rights are associated with attaining the largest or most ferocious trophies (Chase Grey, 2011; Coltman *et al.*, 2003; Kalof and Fitzgerald, 2003). The hunting culture connects with legacies of colonial control over nature and the prestige of hunting the exotic (Swart, 2001). Macho symbols which evoke colonial ideas of conquering nature are also found in other aspects of group A respondents' lives including driving 4 x 4 cars and *braaiing* (barbequing) (Du Pisani, 2001; Van Eeden, 2006).

In North America, the eradication of wolves and other large predators is symbolic of masculinity and class status, as well as a means to protect livestock (Emel, 1998). Killing a wolf is the ideological equivalent of killing a fear of the 'wild', the 'irrational', and the 'different' (Emel, 1998). Some group A respondents boast about which animals they killed and how many, especially in an informal context. Even though many informants are aware that killing certain species is illegal, there are seldom consequences to these actions. Continuing this behaviour and feeling like they beat the system makes people feel untouchable and adds to the machismo effect. Each group suggested that they perceived a different set of laws applied to them. Some group C respondents expressed that they believe they are allowed to kill a leopard

because “the laws are white man laws”. Some commercial farmers believe that they can kill a leopard without being charged because the black government is bribe-able and too lazy to catch them.

After the impala was shot during the biltong hunt I attended, the carcass of the dead impala was taken to the slaughterhouse. The events that unfolded in the slaughterhouse symbolised macho rituals and celebration of human dominance over nature that is unmistakably part of hunting in South Africa. In this excerpt from my ethnographic diary I explain the rituals:

We took it (the impala) to the slaughterhouse. The hunter was given the testicles and a piece of liver which he ate raw later like tradition of your first kill dictates. The professional hunter covered the hunter's face in blood in celebration of his first kill too. The only part of the day I enjoyed less was the trophy photo shoot. It felt so cheesy, fake, conquering. The way the hunter was congratulated - it felt like he was there for the posed photo rather than the meat. There was so much pride.

The tradition of posing proudly in front of a hunted animal in Africa began in the 19th century as a way to convey a message of prowess and dominance (Ryan, 2000). Like a taxidermist mount, a hunters' photograph is a heavily manipulated storytelling device (Goodrich, 2013; Haraway, 1989). By analysing a series of 792 trophy photographs from popular hunting magazines the following undertones were detected: masculinity, racial separation with a strong white male narrative, colonialism, patriarchy, and dominance (Kalof and Fitzgerald, 2003).

Despite recent changes in urban areas (Morrell, 2001), life in the South African bush is still largely male dominated, which perpetuates macho attitudes around hunting and controlling nature (Goodrich, 2013). Women in the Afrikaans culture are typically not involved in farm management or hunting. I identified similar divisions between males and female roles in the Thlane community. Some young Thlane girls told me during their interviews that they feel like they did not have a future other than staying at home and having babies.

Many men in Buysdorp hunt for leisure or food, and some of them belittled hunting on commercial game farms because it is considered unchallenging once the game is farmed and fenced. This extract from my ethnographic diary explains how hunting rituals that are considered macho by one group can be perceived as weak by another.

I asked one of the Buys men how hunting season went. He said badly – he didn't get anything. He expressed how hard it is to get animals, as they are not fenced in. He said he didn't have enough time to do it, as you have to be out from dawn until dusk tracking. He belittled farm hunting as not being real.

By demeaning the valour and skill of hunting on fenced land, the Buys men assert their own masculinity and ability to control nature. Hunting animals establishes authority over nature yet simultaneously it can create supremacy between people within the same societal group or allow people to exhibit power over another group. This illustrates another scenario where a human-animal relationship ultimately has a human-human foundation.

4.3.2.3. A shift from cattle to game farming

In the process of shifting from cattle to game farming, some control over the land and animals is sacrificed back to nature. More environmental variables must be controlled in cattle farming than game farming. For example, domestic animals must be kraaled at night or risk predation, and livestock feed is supplemented throughout the year but especially during the dry winter or periods of drought. Most large game farms conduct aerial game counts annually but this is significantly less intensive monitoring than cattle farming. By shifting to game farming where the bush is left predominantly uncleared and animals are not counted as regularly or cared for as intimately, people loosen control over the land and their animals.

Game farm landowners and managers often have less knowledge about what is happening on their land than cattle farmers because it is harder and less necessary to closely monitor game.

“You know what if we didn’t farm cattle, it (the brown hyaena) wouldn’t worry us at all because we wouldn’t know what it was doing to the game but because cattle is our livelihood we know.” [A36]

Some game farmers feel that it is unfair that unlike cattle farming, there is very little that can be done to protect game animals from predation. However, most game farmers accept an individually defined level of depredation. Game farms are in a more natural state and predation is either considered part of the natural process or game farmers are largely unaware of the extent of losses. The loosening of control is perceived as a liberating process, which brings a greater acceptance towards nature. A province-wide survey indicated that the number of problem animal permit applications lodged by game farmers increased between 2003 and 2012, suggesting that game farmers across a wider area are not as tolerant as I detected on a smaller scale (Pitman *et al.*, 2016b). This may be because most game farmers I interviewed do not breed the highest value game species, and no interviewees breed colour variants or extralimital game species which may be linked to decreased tolerance of predation (Pitman *et al.*, 2016b).

The remaining cattle farmers frequently blame the surge in game farming popularity for higher predator numbers and increases in human-wildlife conflict. It is believed that a province-wide increase in game farms provoked an increase in predators. Game farmers inflict less persecution on predators than livestock farmers (Scriven and Eloff, 2003). Additionally, game farmers often live in Gauteng Province (approximately 359 km away) and are not always on site so they conduct less killing of predators. According to livestock farmers, leopard numbers are thought to have increased because there is less retaliatory behaviour by the more accepting and more remotely situated game farmers. Therefore, when one group releases control over nature, another group can feel forced to tighten their control.

4.3.2.4. Controlling domestic animals and mentally domesticating wild animals

According to Haraway (2008), wild animals free from human domination are the only animals with any form of independent personhood free from human control. Owning an animal makes it seem less wild and imbues a level of power and control to the owner (Haraway, 2008). As part of my participant observation, I volunteered in a slaughter and packing assembly line on a chicken farm in Buysdorp. The chickens are completely utilitarian and live for six weeks, growing from one day old chicks to fully-grown chickens ready for the slaughter. The farmer and farm workers do not have time to grow attached to the chickens or lament their deaths. The sheer volume of chickens on the farm at any one time (~10,000) ensures that. This disconnect contrasts greatly with livestock farming. There is frequently pride in and a connection with domestic livestock. Domestic animals, even cattle, are much more 'part of the family' and more likely to be named and protected. Yet despite this connection, these animals are still seen as a disposable product. While processing chicken carcasses, I contemplated the point when an animal moves from the status of being a live animal to become a product and concluded that these chickens and most livestock are always both.

Game farming centralises around ownership of wild animals and therefore the status of being both an animal and a commodity is bestowed to non-domesticated species. In South Africa through the Game Theft Act and having a certificate of adequate enclosure, all animals found on private land belong to the land's owner (1991). Landowners are quick to claim ownership of a wild animal with financial value such as kudu or nyala, which can be auctioned, hunted, or produce valuable offspring. However, an animal that has lower financial value and causes problems is less likely to be claimed, despite the Game Theft Act. One of the male leopards that I helped to collar through my work with the PPP killed cattle, and in retaliation, he was shot. When I asked the farmer for the collar back, he said that I should have controlled my leopard and demanded compensation from me for his losses. His insinuation that a wild leopard is owned and could be controlled demonstrates how quickly farmers can pass blame in order to regain mental control over their farm management. If the

leopard had value to him, for example through tourism, it is likely that the farmer would have assumed personal ownership instead.

4.4. Summary

Through their presence and actions, brown hyaenas and other large predators can unknowingly obtain power from people across a number of planes. Although brown hyaenas are often acknowledged to be non-problematic animals, many people still have reservations about the species and are uneasy when hyaenas move into human spaces. These uncertainties stem from the brown hyaena's status as a predator and the complex repercussions of unlikely but possible depredation. Certain powerful attributes that are solely assigned to hyaenas, such as their magicality and physical strength, also contribute.

On the surface, farmers' responses appear to focus on regaining power over predators after or in anticipation of a depredation event, yet these actions can often be indicative of deeper human-human power relations. Thus, human-brown hyaena relationships are rooted in human-human relationships. Many of the themes that shape power relations between people and predators hark back to colonial and apartheid disparities, vulnerabilities, and domineering mindsets, similar to how Rust *et al.*'s (2016) intricate web of apartheid invoked inequalities (Figure 4.1) influences human-wildlife conflict in present day Namibia. Fencing and autonomous rule of private, often white-owned properties limit access to nature for poorer black South Africans, mirroring colonial and apartheid divisions (Constant and Bell, in press). Even the ways in which predation events remove control from farmers are reminiscent of the colonial struggle over the land and a survivalist urge to re-establish dominance over nature.

Hunting, largely a pastime of the white community, is connected with management, planning, wealth, historical connections, control, and even conservation. Hunting often requires permission, permits, and careful consideration for the target animal. Culturally, hunting is associated with prestige and honour, especially when the quarry

is a predator. Masculinity and pride associated with hunting lingers from colonialist ideals. In contrast, poaching and snaring, which ultimately have the same physical outcome on the target, are associated with poverty, risk, chance, and elicit behaviour (Lindsey *et al.*, 2013a). Snaring and illegal hunting is one of the only ways many black communities engage with wildlife. Through these poaching practices, power is taken from white or coloured landowners. Violations by trespassers and wildlife thieves on private land are akin to the presence of misbehaving predators.

Power structures between groups swing in both directions, although due to greater access to wealth, education, and land, white people often hold more power. Several group C respondents expressed disdain about how white men claimed land from the black population during colonial and apartheid eras. An attempt to readjust the past and rebalance control is brewing across the country as a whole. In 2015, after a heated protest by students, the University of Cape Town removed a statue of Cecil Rhodes from its campus (BBC News, April 9, 2015). The “Rhodes must fall” movement aimed to remove symbols of colonialism and associated heroic depictions (BBC News, April 9, 2015). Through the land reform programme, the South African government is trying to readdress imbalances in access to land. Land reform is one of the factors that threatens white landowners’ security and makes them feel insecure about their control over their land.

Despite attempts towards greater equality for all people, it is clear that in this postcolonial landscape imperialist undertones and legacies of colonialism still impact many relationships and power structures including human-animal relations, and can provoke both positive and negative effects for wildlife conservation.

Chapter 5: Brown hyaena density and factors affecting occupancy

5.1. Introduction

Although brown hyaenas have the smallest geographic range of all hyaenids (Mills and Hofer, 1998), the areas they occupy are diverse in relation to habitat, climate, altitude, prey distribution, the presence of competitor species, and levels of human influence (Mills and Hofer, 1998). Few studies have examined which factors impact brown hyaena occupancy, yet successful predator conservation is dependent upon determining these factors (Durant *et al.*, 2007; Mills and Gorman, 1997; Singh *et al.*, 2014; Woodroffe and Ginsberg, 1999). In addition, density estimates are vital to indicate whether a carnivore's population is stable or not, and to help define effective conservation management plans (Balme *et al.*, 2009a). The South African national red list assessment for brown hyaenas calls for more density estimates in understudied parts of the species' range, especially in Limpopo and North West Provinces, to improve the accuracy of national estimates and to aid conservation planning (Yarnell *et al.*, in press). This chapter aims to fill gaps in the ecological knowledge on brown hyaena density and the factors affecting their occupancy.

5.2. Occupancy and density estimations

Occupancy modeling is a type of analysis that determines the areas target species occupy and which covariates impact utilisation, through the examination of detection/non-detection data (MacKenzie *et al.*, 2006; O'Connell and Bailey, 2011). Occupancy is based on the presence and absence of a species at given locations rather than the occurrence of specific individuals (MacKenzie *et al.*, 2006). Each sampling location has a unique set of features (site covariates) which define it and are tested against occupancy estimates (the probability that a species is present at a site) and probabilities of detection (the probability that one or more individual of a species will be detected, provided the species resides in the area) to determine the extent to which certain features affect a species' use of space (MacKenzie *et al.*, 2006).

Density is defined as the number of individuals of a species within a unit area (Long and Zielinski, 2008) and is commonly expressed in terms of a universal measurement (Long and Zielinski, 2008). Through continued density monitoring over time, population trends can be detected (Karanth *et al.*, 2006; Long and Zielinski, 2008). Population estimates at one site can be compared to densities elsewhere to make assumptions about conditions affecting population health (e.g. Kelly *et al.*, 2008; Swanepoel *et al.*, 2015).

5.2.1. Factors affecting brown hyaena occupancy

A variety of factors affect predator density, distribution, and occupancy, many of which are interlinked and can create knock on effects elsewhere within the system (Mills, 1991, 2005; Miquelle *et al.*, 2005; Sunarto *et al.*, 2012; Winterbach *et al.*, 2014; Winterbach *et al.*, 2013). In occupancy analysis, covariate selection and hypotheses about covariate effects are based on previous knowledge of a species and its environment (MacKenzie *et al.*, 2006; Nijhawan, 2010). In this section, I justify site covariate selection and hypotheses tested in the occupancy study.

As a scavenger, the brown hyaena has a more versatile diet than exclusively predatory carnivores, which consists of carrion, insects, fruits, and eggs (Burgener and Gusset, 2003; Mills and Mills, 1978; Owens and Owens, 1978). However as confirmed in Chapter 7, the majority of their diet is composed of medium to large sized mammals (Burgener and Gusset, 2003; Maddock, 1993; Mills, 1982a; Owens and Owens, 1978; Slater and Muller, 2014; van der Merwe *et al.*, 2009; Yarnell *et al.*, 2013). As prey biomass levels positively affect the density of carnivores (Kruuk and Parish, 1982; Van Orsdol *et al.*, 1985), I hypothesise that brown hyaena occupancy and probability of detection will be higher in areas where more prey is available.

Dominant predators can present a threat for submissive carnivores. In areas of Kruger National Park with the highest prey abundance for African wild dogs, wild dog density is the lowest due to the presence of more dominant carnivores in these areas such as lions and spotted hyaenas (Mills and Gorman, 1997). Wild dogs therefore shift their

ranges to seek prey elsewhere and avoid potentially debilitating or fatal competition (Mills and Gorman, 1997). The use of 'competition refuges' by cheetahs has also been recorded in the Serengeti (Durant, 1998) and in reserves within South Africa (Cristescu *et al.*, 2013).

Carnivores that are predominantly hunters are dependent upon prey size and relative abundance, and therefore must avoid competition from other predators. The effects of interguild interactions become more apparent when an apex predator is removed. Apex predators often suppress smaller mesopredators by killing them, triggering fear based behaviour, and limiting access to prime foods or habitats (Ritchie and Johnson, 2009). In the absence of apex predators, mesopredator populations will frequently expand to fill their niche and surge in numbers through the mesopredator release effect (Crooks and Soulé, 1999). This population increase is attributed to a greater supply of food sources with less competition (Crooks and Soulé, 1999). As apex predators decline worldwide, the mesopredator release effect is likely to intensify, affecting ecosystem stability through greater predation of smaller prey and increases in the populations of larger herbivores (Ritchie and Johnson, 2009; Sergio *et al.*, 2008).

Little is known about the complexity of relationships between animals that are predominantly scavengers and other predators. In a study of African carnivores, the brown hyaena ranks highly for the number of competitor species ($n = 8$) that steal food from them (Caro and Stoner, 2003). However, this study did not investigate the inverse situation whereby the brown hyaena acts as a potential kleptoparasite on other carnivores, which experience greater vulnerability to theft such as the leopard and black-backed jackal (Caro and Stoner, 2003). Both of these species have an estimated 13 competitor species stealing from them, one of which is the brown hyaena (Caro and Stoner, 2003). The brown hyaena's opportunistic nature may allow them to exploit a wider resource base and therefore they may have a lower dependency level upon prey. Additionally, their relationships with other predator species are complex, as these species do not necessarily act as competitor species, which would negatively affect a hyaena's access to resources. Alternatively, other predator species provide a food source and may have a positive effect on brown hyaena feeding success (Slater and Muller, 2014; Yarnell *et al.*, 2013). Brown hyaena

density is higher in an apex predator rich area which has greater scavenging opportunities than in an similar area lacking competitor species (Yarnell *et al.*, 2013). In predator rich areas, brown hyaenas have a more varied diet and are in less direct competition with another mesopredator, the black-backed jackal (Yarnell *et al.*, 2013). In areas where leopard are present, brown hyaenas have a very similar diet to them (Stein *et al.*, 2013). This is explained by a high frequency of observed scavenging incidents from leopard kills (76%) (Stein *et al.*, 2013). It is therefore presumed that the presence of large predators such as leopards will have a positive effect on brown hyaena occupancy and probability of detection.

In North West and Limpopo Provinces, brown hyaena relative abundance is four times lower in unprotected areas than protected areas despite more plentiful food resources in unprotected areas (Richmond-Coggan, 2014). Brown hyaena occupancy is higher in protected areas compared to farming areas in North West Province (Thorn *et al.*, 2011a). Higher human persecution levels is the probable driving factor behind this trend (Richmond-Coggan, 2014). Human impact may affect predator distribution and density directly (e.g. through persecution of predators) but also indirectly by affecting habitat structures or prey availability (e.g. through activities such as hunting, snaring, and habitat destruction) (Johnson *et al.*, 2006; Williams, 2011; Williams *et al.*, 2016; Woodroffe, 2000). Prey numbers are often significantly lower in areas of high human influence which has a knock on effect on predator distribution and abundance (O'Brien *et al.*, 2003). Leopards in Armenia have a lower than expected density level when compared to the expected carrying capacity that the estimated total ungulate prey biomass is predicted to be able to support (Khorozyan *et al.*, 2008). A high level of human influence on the environment and frequent conflict is the most likely explanation for this discrepancy (Khorozyan *et al.*, 2008). Human-induced habitat destruction is linked to lower predator occupancy levels (Gerber *et al.*, 2012) and reduced prey availability can place a greater strain on interspecific competition (Johnson *et al.*, 2006), illustrating how various factors can become interwoven.

Human activity does not always equate to lower predator densities and reduced distribution, as large predators can sometimes coexist with people on a fine spatial scale (Athreya *et al.*, 2013; Carter *et al.*, 2012). In the Kgalagadi Transfrontier Park,

brown hyaenas adapt to human activities better than many other carnivores, including the spotted hyaena (Mills, 1990). In Pilanesberg National Park, South Africa, distance from disturbed sites (areas with high human activity associated with tourism) does not affect brown hyaena occupancy (Thorn *et al.*, 2009). This is probably because the brown hyaena population is in a protected area where high human activity does not pose a dangerous situation for brown hyaenas. Outside of protected areas, brown hyaena density is high on livestock and game farms (Boast and Houser, 2012) with slightly higher numbers on livestock farms (Kent and Hill, 2013). Vulture restaurants on private land can increase brown hyaena abundance (Yarnell *et al.*, 2014). These findings contradict with the lower brown hyaena abundance found on unprotected land by Richmond-Coggan (2014), and may be explained by geographic variation. It is predicted that despite hyaenas' resilience to human impact, predator persecution, especially from indirect causes, at the study site (Chapters 3 and 4) will result in lower occupancy levels where human activity is high. It is also anticipated that brown hyaenas' probability of detection will be higher in areas with lower human activity, similar to finding by Carter *et al.* (2012) that tiger detection probability increased with distance to human settlement.

High densities of brown hyaenas found on livestock farms in Botswana (Boast and Houser, 2012; Kent and Hill, 2013) contrast with the lower occupancy and abundance of brown hyaenas in farming areas compared to protected areas in South Africa (Richmond-Coggan, 2014; Thorn *et al.*, 2011a). These differences may be attributed to variations in cattle management and a much lower human population density in Botswana (Kent and Hill, 2013). In Botswana, graze is sparse and small herds of livestock are often left to roam with little human supervision (Kent and Hill, 2013). In and around the Soutpansberg Mountains, tolerance towards brown hyaenas is lower on livestock farms compared to game farms or tourism areas (Chapter 3), therefore it is assumed that conditions will be more closely aligned with studies conducted within South Africa, and brown hyaena occupancy and probability of detection will be lower where there is more livestock.

Brown hyaenas have great spatial needs due to their large home ranges (Maude and Mills, 2005; Mills, 1983; Owens and Owens, 1996; Wiesel, 2006) and sizeable roaming

distances of up to 50 km a night (Mills, 1990). Overall, game farmers interviewed in Chapters 3 and 4 have larger sized properties than livestock farmers or tourism operators. It is therefore assumed that brown hyaena occupancy will be higher on larger properties because these areas align more closely with brown hyaenas' spatial needs and once on a larger property, the necessity to move in and out of more dangerous zones is lower. However, a singular property in the study area is not large enough to fulfil all the spatial needs of a brown hyaena, therefore hyaenas need to cross onto different properties (Chapter 6). Brown hyaenas transverse game and cattle fences on a regular basis through holes underneath dug by warthogs, aardvarks (*Orycteropus afer*), or other brown hyaenas (Kesch *et al.*, 2013; Richmond-Coggan, 2014; Wiseman Jones, 2014). Due to this unimpeded movement, I predict that fence presence and type will not have an effect on brown hyaena occupancy. However, probability of brown hyaena detection is predicted to be higher along fencelines because the area adjacent is clear from vegetation, which creates a fast and visible corridor of movement.

Habitat and environmental factors greatly influence prey biomass and biodiversity levels (Fahrig, 2003; Swanepoel *et al.*, 2013; Swihart *et al.*, 2001), which in turn can impact interspecific competition or scavenging opportunities. Leopards living in northern Limpopo Province are more likely to be detected in forest/woodland compared to thicket/bushland (Constant, 2014). The study by Constant (2014) was conducted in a similar geographic area to this thesis, and due to the overlap between leopard and brown hyaena diet (Stein *et al.*, 2013), it is hypothesised that brown hyaenas will also be detected at higher rate within closed habitats. This hypothesis corresponds with a finding by Thorn *et al.* (2009) that brown hyaena detection is higher in denser areas of scrub or woodland rather than grasslands. Habitat did not affect occupancy (Thorn *et al.*, 2009) and the same outcome is predicted in this study.

Brown hyaenas utilise flatland and montane areas (Hulsman *et al.*, 2010; Mills and Mills, 1982; Skinner, 1976; Wiesel, 2006). One study concluded that brown hyaenas favour mountainous areas with bush cover (Skinner, 1976). This finding is attributed to seclusion, safe hiding places, and the lack of human disturbance (Skinner, 1976). Based on interviews (Chapter 3), anthropogenic risks are lower in the Soutpansberg

Mountains than the neighbouring flatlands. Additionally, leopard density and therefore scavenging opportunities are high in the mountainous areas (Chase Grey *et al.*, 2013). It is predicted that brown hyaena occupancy will be higher at camera traps placed in the mountains than stations in the flatlands.

5.2.2. Hypotheses influencing covariate selection for occupancy modeling

Guided by established ecological information about the study species (MacKenzie *et al.*, 2006; Nijhawan, 2010) outlined in section 5.2.1, site covariates in occupancy modeling test eight hypotheses within a strategic multiple-hypothesis approach (Table 5.1) (Burnham and Anderson, 2002; Negroes *et al.*, 2010).

Table 5.1 Hypotheses influencing covariate selection.

Hypotheses
5.1 Brown hyaena occupancy and probability of detection is higher in areas where prey activity levels or biomass estimates are higher.
5.2 Brown hyaenas occupancy and probability of detection increases in areas with higher predator numbers.
5.3 Brown hyaena occupancy and probability of detection is lower in areas of high human activity and high human-hyaena conflict.
5.4 Brown hyaena occupancy and probability of detection is lower in areas of high livestock abundance.
5.5 Brown hyaena occupancy is higher on larger farms.
5.6 Brown hyaena occupancy is not affected by fence presence and type. Probability of detection is higher where there are fences, regardless of type.
5.7 Habitat does not affect brown hyaena occupancy. Probability of detection is higher in areas with thicker bush.
5.8 Brown hyaena occupancy is higher in montane environments

5.2.3. Brown hyaena population densities

The accuracy of estimating brown hyaena density is questionable because of difficulties in confirming brown hyaena presence within a sampling area. Brown

hyaenas are often overlooked due to their secretive nature and nocturnal habits (Mills and Hofer, 1998; Stuart *et al.*, 1985).

The challenges of recording brown hyaena presence and the understudied nature of the species have resulted in relatively few density estimates, especially using the robust spatially explicit capture recapture (SECR) methodology (Table 5.2). The majority of studies calculated brown hyaena populations in protected areas where brown hyaenas encounter low levels of anthropogenic activity or human conflict (Table 5.2). Generally brown hyaena density is higher on protected land compared to non-protected areas (Thorn *et al.*, 2009; Yarnell *et al.*, 2013). To date, brown hyaena density has been calculated in just two semi-montane areas – Pilanesberg National Park and the neighbouring Mankwe Reserve (Thorn *et al.*, 2009; Yarnell *et al.*, 2013) – and only one study includes closed woodland habitats (Welch and Parker, 2016).

Table 5.2 Brown hyaena density estimates.

Study	Location	Habitat	Human impact	Brown hyaena density estimate / 100 km ²	Methods
Boast and Houser (2012)	Ghanzi, Botswana	Semi-arid brush to open tree savanna	High impact: cattle, game, and mixed commercial farming	2.18	1
Kent and Hill (2013)	Ghanzi, Botswana	Semi-arid brush to open tree savanna	High impact: cattle, game, and mixed commercial farming	2.3 – 2.88	2
Maude (2005)	Makgadikgadi National Park and neighbouring cattle area, Botswana	Short grasslands and saline pans	High impact and low impact: cattle farming and national park	Up to 2	3
Mills (1990)	Kgalagadi Transfrontier Park, South Africa/Botswana	Sand-veld semi-desert	Low impact: tourism only	1.8	4

Study	Location	Habitat	Human impact	Brown hyaena density estimate / 100 km ²	Methods
Thorn <i>et al.</i> (2009)	Pilanesberg National Park, South Africa	Open grassland with thickets of <i>Acacia</i> and broadleaf bushveld	Low impact: tourism only	2.8	5
Welch and Parker (2016)	Kwandwe Private Game Reserve, South Africa	Great Fish Noorsveld and Great Fish Thicket	Low impact: tourism only	14 – 20	5, 6
Wiesel (2006)	Van Reenen Bay, Namibia	Coastal sandy/rocky desert	Low impact: in national park, human access minimised for coastal mining	1.0 – 1.6	7
Wiesel (2006)	Baker's Bay, Namibia	Coastal sandy/rocky desert	Low impact: in national park, human access minimised for coastal mining	2.4 – 2.9	7
Yarnell <i>et al.</i> (2013)	Pilanesberg National Park, South Africa	Open grassland with thickets of <i>Acacia</i> and broadleaf bushveld	Low impact: tourism only	6*	8
Yarnell <i>et al.</i> (2013)	Mankwe Wildlife Reserve, South Africa	Open grassland with thickets of <i>Acacia</i> and broadleaf bushveld	Low impact: tourism only	2 – 4*	8

*Data extrapolated to reflect a density of 100 km² from original estimate based on 1 km².

Methods used: 1 - Spoor sampling and calibration, 2 – SECR analysis using SPACECAP, 3 – Extrapolated from home range sizes of GPS collared animals in Thorn *et al.* (2009), 4 - Extrapolation from average territory and group size, 5 – CAPTURE analysis, 6 – SECR analysis using DENSITY, 7 - Extrapolation from abundance estimates and home range sizes of GPS collared animals, 8 - Identified individuals from

camera trap data, calculated minimum number alive per month, and estimated total number of individuals using the site.

Brown hyaena density estimates averaged 2.8 individuals per 100 km² if Kwandwe Private Game Reserve is excluded. The very high density estimates at Kwandwe Private Game Reserve may be attributed to the differing habitat type, an abundance of food resources, optimal scavenging opportunities, the secure enclosure of the reserve, or a combination of several factors (Welch and Parker, 2016).

5.3. Methods

5.3.1. Camera trapping

Camera trapping is one of the most effective methods of counting cryptic carnivores (Balme *et al.*, 2009a; O'Connell *et al.*, 2011) and is an increasingly popular methodology in carnivore ecology (McCallum, 2013). Camera traps are commonly used to generate the data required to determine occupancy (Gerber *et al.*, 2012; Linkie *et al.*, 2007b; Negroes *et al.*, 2010; O'Connell and Bailey, 2011; Shannon *et al.*, 2014; Thorn *et al.*, 2009) and density (Foster and Harmsen, 2012; Noss *et al.*, 2012; O'Brien, 2011; Singh *et al.*, 2014; Soisalo and Cavalcanti, 2006).

I conducted two camera trapping surveys employing different methodologies in this study: camera trapping for occupancy analysis and camera trapping for spatially explicit capture recapture analysis.

5.3.1.1. Camera trapping for occupancy

This survey used 20 no-glow infrared camera traps (Reconyx Hyperfire™ HC600, Reconyx Inc., Holmen, WI, USA). Reconyx cameras have the fastest trigger speed and the lowest recovery time of all camera traps available on the market which results in a high photographic capture rate (Trolliet *et al.*, 2014). However, a preliminary assessment of brown hyaena photographs taken using these cameras determined that

the photographic quality was not sufficient to individually distinguish hyaenas. Brown hyaenas move very quickly past the cameras and although the cameras' fast trigger speed captured the animals, numerous images were blurry and unusable for individual identification (Figure 5.1). Brown hyaenas can be identified by their unique leg stripe patterns and sometimes by naturally formed ear notches (Kent and Hill, 2013; Wiesel, 2006). These identifiers are clearly visible in photographs taken by camera traps with a visible light flash (Figure 5.2). Infrared cameras produce colour images in the day but at night when hyaenas are active, photographs are in black and white (Trollet *et al.*, 2014), which amalgamates important differences in fur colouration.



Figure 5.1 Example of a camera trap photograph of a fast-moving brown hyaena taken with a Reconyx HC 600 infrared camera in the Soutpansberg Mountains. Although the species is clearly identifiable, the features needed to recognise individuals (leg stripes and ear notches) are out of focus.



Figure 5.2 Photograph of a fast-moving brown hyaena at night taken with a visible light flash camera trap (Panthera V4, Panthera, New York, NY, USA) in the Soutpansberg Mountains. The distinctive stripe patterns on the front and back legs and clear view of the ears allow for individual identification.

I set up the first camera trapping study to address research aims while accommodating the limitations of the equipment available. Occupancy was an appropriate approach for this camera trapping study because it examined anthropogenic and environmental variables affecting brown hyaena distribution without requiring individual identification (MacKenzie *et al.*, 2006).

One of the conditions of occupancy is that sampling points - camera trap stations in this instance - need to be widely spaced to ensure that at least an entire home range of the target species can fit in between (Boitani *et al.*, 2012; Long and Zielinski, 2008; MacKenzie *et al.*, 2006). This guarantees that the same individual is not sampled at more than one point and locational detection histories are independent (Boitani *et al.*, 2012).

I used global positioning system (GPS) data collected from one of the brown hyaenas I collared as part of this study to calculate a locally accurate home range based on minimum area convex polygons (MCP) (Chapter 6). The widest distance between any two GPS points within the largest territory was 22.3 km. Thus, all cameras were spaced apart by at least 22.3 km to ensure sampling independence.

Using Quantum GIS v 2.6 (Quantum GIS Development Team, 2014), I mapped out a 5 x 4 grid based on the prescribed camera spacing. The grid extended across the top of the Soutpansberg Mountains and areas to the north and south of the mountains to allow comparison of brown hyaena occupancy between mountainous and low-lying areas (Figure 5.3).

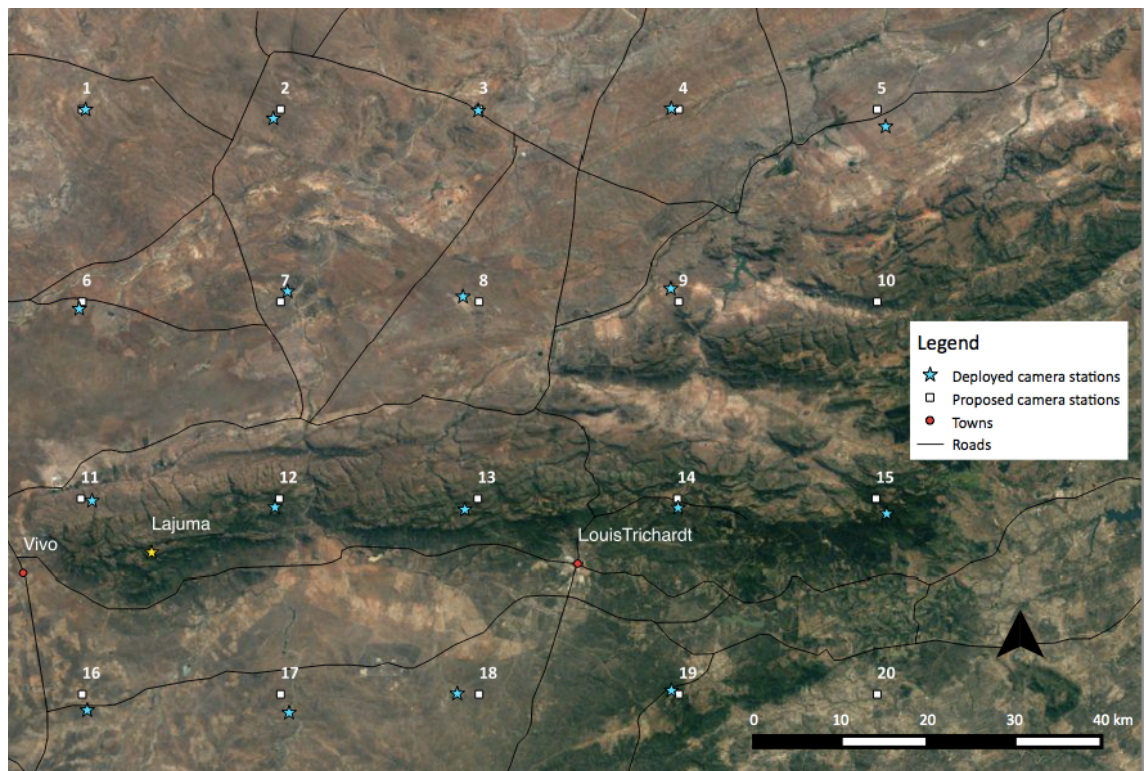


Figure 5.3 Map of occupancy camera trapping grid showing deployed and proposed camera stations in and around the Soutpansberg Mountains. Camera station numbers are indicated next to the station. Station 10 was removed partway through the study due to repetitive camera failure. Station 20 was never established because this point ended up in a township. Roads indicate tarred roads.

I visited each suggested point and acquired permission to place a camera trap from landowners. At each computer-generated point, I searched within a 2.5 km radial buffer for an appropriate position to place my camera station (Figure 5.3). For

occupancy analysis, sampling points must be placed where there is reasonable probability of detecting target species to reduce inaccuracies in analysis stemming from false absences, but points should not be selected where detection is guaranteed (MacKenzie *et al.*, 2006; Mackenzie and Royle, 2005). An open savannah with no game trails or roads is not an appropriate location for a camera station because there is no reason why a hyaena would walk in one spot over another, therefore hyaenas might be present in the vicinity but may never be detected on the camera, creating a false absence. A camera placed at the side of a clearly utilised walkway is a better placement as predators will actively move there, increasing the chance of capture (Gese *et al.*, 2012). Positions that met the above criteria were acquired for all points barring one. One point was omitted from the study because the spot and the surrounding area are in a densely populated township (station 20). Due to the location's high human population and human-dominated landscape there was not a reasonable chance a brown hyaena could be detected there.

I placed cameras in metal boxes for security and locked them to trees two or three metres back from the road/track at a height of about 45 centimetres above the ground (Karanth, 1995; Kelly *et al.*, 2008; O'Brien *et al.*, 2003; Thorn *et al.*, 2009). I removed all vegetation that might move in the wind and cause the camera to trigger from the area (Swann *et al.*, 2004). I downloaded data, replaced rechargeable batteries, and cleared sprouting vegetation from the sites on a monthly basis.

A pilot period of 40 days trialled predator detection at selected locations and allowed adjustment of cameras to their final positions. For optimal occupancy results, sampling should be conducted during closed population periods (Boitani *et al.*, 2012; Long and Zielinski, 2008; Rota *et al.*, 2009). By sampling for a short period of time, the assumption that animals do not experience immigration, emigration, mortality, or recruitment can be met (Karanth and Nichols, 1998). I designated a survey length of 66 continuous camera trapping days (following Constant, 2014; Kent, 2011). However, due to technical problems with multiple camera traps, meeting this goal was delayed and only achieved between June 23, 2014 and August 27, 2014 after replacing several cameras and removing a problematic station from the grid (station 10). After altering the grid to accommodate faulty cameras and unused stations, the area surveyed

covered 5,431 km² (Figure 5.3). As brown hyaenas are relatively common and moderately detectable, the low number of cameras ($n = 18$) and the short sampling period is sufficient to provide a reliable occupancy estimate (Shannon *et al.*, 2014).

At each station, I recorded geographic characteristics including habitat, altitude, and location in relation to the Soutpansberg Mountains. I assessed habitat within a 25 m radius from the camera station by eye and categorised areas as mostly open/grassland, mix of woodland/grassland, or mostly closed/woodland. I took photographs of the area surrounding each station to reconfirm habitat classification decisions in comparison with all sites later.

5.3.1.2. Camera trapping for spatially explicit capture recapture

I developed a second camera trapping survey to meet the criteria for spatially explicit capture recapture (SECR) analysis.

Panthera, an international felid conservation organisation, established the Limpopo Leopard Project in 2013 in partnership with the Limpopo Department of Economic Development, Environment, and Tourism (LEDET) and the University of KwaZulu-Natal to monitor leopard populations across Limpopo Province and influence conservation initiatives. In August 2014, the Primate and Predator Project (PPP) joined this collaboration. The PPP agreed to lead a camera trapping survey across an approximately 220 km² area spanning the north and south slopes of the western Soutpansberg Mountains (Figure 5.4) for approximately two-month periods on an annual basis for a decade. Although the camera trapping grid was set up for leopard monitoring, Panthera granted me permission to use the images of brown hyaena collected in the western Soutpansberg Mountains in this study. At the start of the second year of the study, we moved four camera stations from the western end of the study area to the eastern section (Figure 5.4) due to a landowner's decision to cease involvement, resulting in a 200 km² grid in 2015.

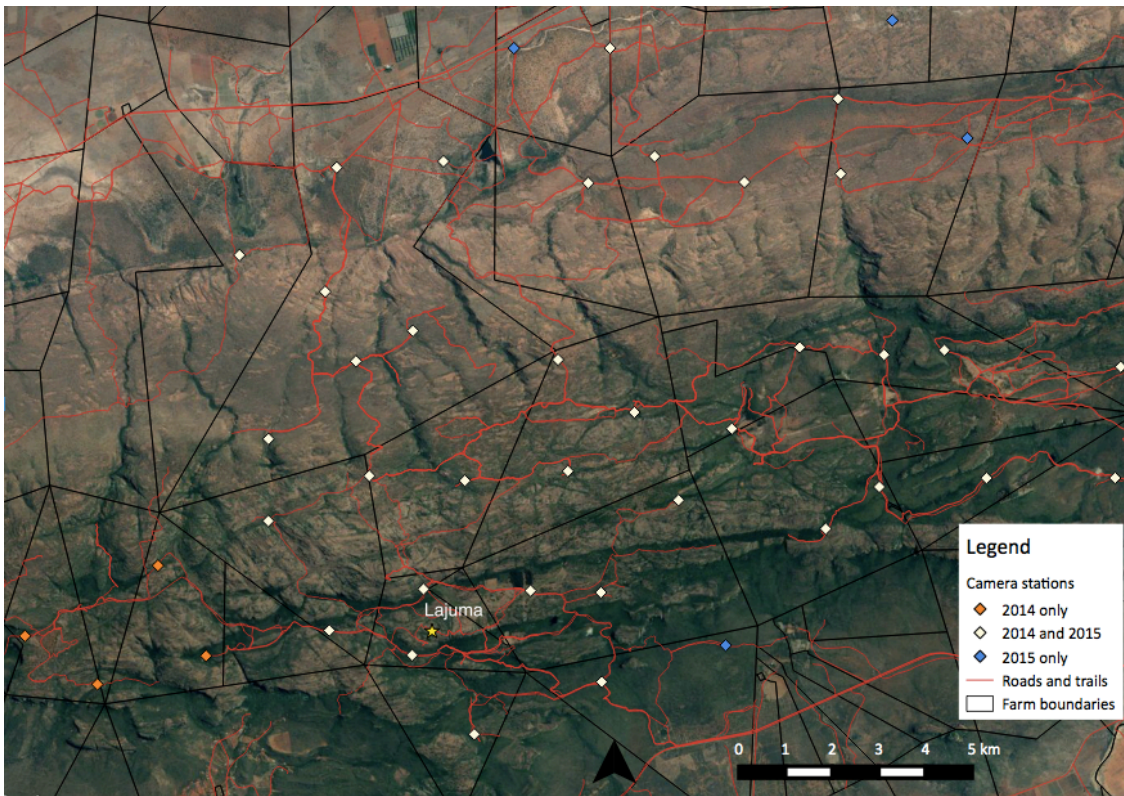


Figure 5.4 Map of the SECR camera trapping grid set up by the PPP and Panthera in the western Soutpansberg Mountains. Differences in camera station locations between 2014 and 2015 are indicated by symbol colouration.

I established and maintained the camera trapping grid, which hosted 80 camera traps (Panthera V4, Panthera, New York, NY, USA). Cameras were set up in paired sets at 40 stations to aid individual identification of predators (Negroes *et al.*, 2012). Each pair of cameras faced each other with a lateral offset of between 0.5 to 1 m. Staggering is recommended to reduce the flash overexposing the opposite camera's photos (Sollmann *et al.*, 2011). Distance from the road and height above the ground was similar to that described in the occupancy survey. I replaced batteries, downloaded data, and cleared vegetation on a fortnightly basis.

Cameras were spaced at a maximum of three kilometres from each other to ensure that all leopards in the study area have the opportunity to be photographed (Figure 5.4). The average home range of a female leopard in this area is 20 km² (n = 2, 95% MCP) (Swanepoel *et al.*, 2016). Male leopards have significantly larger home ranges - on average 100 km² (n = 5, 95% MCP) (Swanepoel *et al.*, 2016). If no camera station is further than three kilometres in any direction from neighbouring stations, no holes in

the study area will be large enough to exclude a female leopard's territory (Karanth *et al.*, 2011b). Although this grid was set up for leopards, the spacing is also appropriate for brown hyaena SECR analysis because the home range of male and female brown hyaenas (Chapter 6) are larger than a male leopard's, therefore every hyaena passing through the sampling area has the chance to be photographed.

The cameras utilised in this survey are not available on the commercial market. They were specifically designed and produced for Panthera. The cameras have quick visible light flashes and therefore they take colour photographs both day and night. They have a longer delay between photographs than infrared cameras – about eight seconds compared to less than one second on the occupancy grid. The delay means that only one image is normally captured per animal moving through rather than a series of photos, but the quality of the image at night is significantly better (Figure 5.2). The majority of brown hyaenas photographed could be individually identified by their markings, which is a condition of SECR analysis (Karanth, 1995; Karanth and Nichols, 1998; Noss *et al.*, 2012).

A closed population is also a requirement of SECR and datasets of 46 and 49 days were analysed (August 23 - October 7, 2014 and February 17 - April 6, 2015). The length of sampling was short enough to justify a closed population but long enough for individuals to be photographed several times (Kays and Slauson, 2008).

5.3.2. Questionnaires to accompany the occupancy survey

The occupancy camera trapping survey covered a vast and ecologically diverse area (Figure 5.3). Information on human activity, land use, domestic animal numbers, problems with predators, and perceptions of hyaenas at each station was not always visually apparent. I administered questionnaires to the property owners to gather these site-specific data (Appendix 4).

All camera stations were on private land owned by English or Afrikaans-speaking owners. Questionnaires were available in these two languages. The questionnaires

requested information on lethal control of hyaenas. I guaranteed participants anonymity in their answers.

Self-completion questionnaires are useful ways to gain information but can sometimes produce a low response rate and questions can be misinterpreted (Aldridge and Levine, 2001; Cloke *et al.*, 2004; May, 1993; van der Waal and Dekker, 2000). I dispensed questionnaires after several monthly camera trap checks to ensure that I had developed a rapport with landowners. Consequently, participants had a better understanding of the research and felt connected with my work, increasing their motivation to complete the questionnaire properly and return it. All landowners submitted questionnaires.

5.3.3. Data analysis

5.3.3.1. Sorting camera trap images

I prepared images collected as part of the occupancy study and the SECR study for analysis using similar methods. Each photograph was individually examined. I deleted any pictures that did not show an animal, a human, or a vehicle. All remaining photos were tagged with a descriptive tag indicating the species depicted, human, or vehicle in Windows Live Photo Gallery (Microsoft Corporation, Redmond, WA, USA).

The SECR survey required an additional step. I tagged each brown hyaena photograph with a supplementary label denoting the identity of the individual pictured. To aid identification, I produced a booklet with ID photos which clearly featured leg stripes and ear notches for each brown hyaena recorded (Figure 5.5).



Figure 5.5 Matching ear notches and leg stripes on a brown hyaena photographed at different stations and on different days during the same SECR survey.

Distinguishing between individual brown hyaenas using unique leg stripes and ear notches is more challenging than identifying animals with more distinct full body pelage such as leopards and jaguars (Kent and Hill, 2013). Consequently, two to three independent research assistants checked all brown hyaena identification assessments and I made the final assessment. I excluded any images that were not clear enough for definitive identification from the analysis (Karanth *et al.*, 2011b). All brown hyaenas photographed were adults, so no images were omitted because of the presence of cubs or subadults. Frequently, young animals are excluded in SECR analysis because they have low capture probabilities (Karanth, 1995).

Although the SECR camera trapping array was set up with two opposing cameras per station, occasionally only one flank of an animal was photographed. In situations where photographs showed only one side of the animal, I included only the most commonly photographed set of singular flanks (left or right) to avoid artificially elevating population estimates by counting an animal's left and right flanks as two separate individuals (Kent and Hill, 2013; Singh *et al.*, 2010; Singh *et al.*, 2014).

Once all images had been tagged, the metadata embedded in the images and inserted during the tagging process was extracted using ExifTool 9.78 (Harvey, 2014). The metadata was saved in a Microsoft Excel worksheet (Microsoft Corporation, Redmond, WA, USA).

5.3.3.2. Occupancy

I included all camera trap images aside from empty frames and unidentifiable species in analysis. The extracted metadata from all useable camera trap images was prepared for inputting into PRESENCE v 10.2 (MacKenzie, 2016).

I created a detection history comprised of 0 and 1s to reflect brown hyaena presence and absence across the 18 camera stations over 11 six-day sampling periods. The length of a sampling period is defined based on the rarity of the study species (O'Connell and Bailey, 2011). Many camera trapping studies consolidate data into cumulative segments of between four and seven days (Constant, 2014; Erb *et al.*, 2012; Kent, 2011; Negroes *et al.*, 2010; Tobler *et al.*, 2009). This length of time is easy to manage and does not over or under compress the statistical power of the data (Erb *et al.*, 2012). The frequency of sampling also fits with the assumption that more commonly detected species such as brown hyaena should be monitored across a smaller area more frequently in contrast to rare species which should be sampled less frequently across a wider area (Mackenzie and Royle, 2005; Shannon *et al.*, 2014). The following x-matrix [00101000000] indicates that at a particular site, a brown hyaena was seen at least once during the third and fifth sampling intervals (Otis *et al.*, 1978).

During all other intervals, no brown hyaena activity was recorded. A zero may happen when the species is absent from the site or a false absence occurs - an animal is present but is not detected during sampling (MacKenzie *et al.*, 2002; Royle and Dorazio, 2008).

Camera trapping has a very small sampling range compared to other methods such as auditory counts, which detect species across a wider area (Efford and Dawson, 2012). Therefore, a brown hyaena may be present in the general area but avoid the immediate vicinity of the camera or the camera may not have captured the animal due to a malfunction during the sampling period. Compensating for potential false absences is an essential function of occupancy analysis which distinguishes between a naïve occupancy estimate and the best estimate of occupancy (MacKenzie *et al.*, 2006). I tested a number of site covariates (Appendix 5) against the hypotheses in Table 5.1 for significance on brown hyaena occupancy and probability of detection.

I calculated prey, predator, and human activity levels based on the photographs taken at each station. However, the total number of raw photographs of all species and vehicles taken at each station does not reflect a true level of activity (Rovero *et al.*, 2005). Some species such as chacma baboons produced high numbers of photographs due to their large group sizes and tendency to play in front of the cameras for long periods of time. Species such as black-backed jackal were also frequent visitors to the cameras, but as an often solitary (Smithers, 1986) and highly mobile species (Botham, 1971), they produced less photographs. To ensure independence between photographic events and create a comparable baseline, photographs of the same species taken at the same station occurring within a 60-minute interval were grouped as a single capture event (Bowkett *et al.*, 2008; Negroes *et al.*, 2010; Rovero and Marshall, 2009; Tobler *et al.*, 2009).

Capture frequencies were used to calculate the number of independent photographs per 100 camera trap days using a relative abundance index (RAI) (Jenks *et al.*, 2011; Negroes *et al.*, 2010; O'Brien *et al.*, 2003; Treves *et al.*, 2010). A camera trap day is defined as a 24-hour period when the camera station was fully functional (Meek *et al.*,

2014). In the case of a group living animal, group size was included in the RAI equation:

$$RAI_i = \left(\frac{g_i \sum_j P_{ij}}{\sum_j tn_j} \right) * 100$$

where g_i is the average group size for i th species, P_{ij} is the number of independent captures for i th species at j th camera trap location, and tn_j is the total trap-days at the j th camera trap location (Kawanishi and Sunquist, 2004; Khorozyan *et al.*, 2008; Li *et al.*, 2010; Negroes *et al.*, 2010; O'Brien *et al.*, 2003).

Group size varies considerably between geographic areas depending upon factors such as habitat, food availability, and predation risk (Langen and Vehrencamp, 1998; Matsumoto-Oda *et al.*, 1998; Mills, 1982a). Additionally, group size is carefully controlled on private land through game management (Bothma *et al.*, 2009) and this was a consideration in my study. Therefore, a survey specific approach to estimating group size was necessary. I examined every photograph taken featuring an animal and recorded the number of individuals per frame. From this information, I produced an average individual per frame estimate for all species at every station (following Kent, 2011). One of the constraints of this method is that large sized animals such as cows and greater kudus, and animals living in very large groups such as chacma baboons, are likely to be underestimated (Kent, 2011). Nevertheless, this is the most robust approach available as it effectively counters some detectability biases in camera trapping (e.g. O'Brien *et al.*, 2003; Tobler *et al.*, 2008; Treves *et al.*, 2010).

I defined prey species for inclusion from brown hyaena dietary literature (Burgener and Gusset, 2003; Maddock, 1993; Maude, 2005; Mills and Mills, 1978; Owens and Owens, 1978; Siegfried, 1984; Skinner and Van Aarde, 1981; Skinner *et al.*, 1995; Stein *et al.*, 2013; Stuart and Shaughnessy, 1984; van der Merwe *et al.*, 2009). Following studies undertaken in areas where predators live in close proximity to humans, domestic dogs and livestock were included as potential prey species (Athreya *et al.*, 2013). To accommodate for locally specific feeding behaviour, I also based potential prey species on scat analysis results (Chapter 7).

I inputted the RAI values per species at each station as site covariates into the occupancy analysis. I calculated the biomass abundance indices (BAI) per species and per station by multiplying the RAI by each species' average female body weight (Negroes *et al.*, 2010). I acquired these weights from regionally specific literature (Skinner and Chimimba, 2005; Stuart and Stuart, 2007). Utilising female weight or 0.75 x female weight compensates for size variation between the weights of all individuals photographed (Hayward *et al.*, 2006; Treves *et al.*, 2010). Once computed, I inputted BAI estimates as site covariates in PRESENCE v 10.2 (MacKenzie, 2016).

I calculated RAI and BAI estimates at an independent species level and subsequently conjoined them to formulate pertinent groups. Data was combined into taxonomic and size-based categories such as antelopes, birds, primates, very small prey (average female weight <1 kg), small prey (average female weight 1-15 kg), medium prey (average female weight 15-50 kg), and large prey (average female weight >50 kg). Prey size groupings were based on brown hyaena dietary classifications by Mills and Mills (1978).

I standardised RAI and BAI values as z-scores due to the large range of values present (following Harihar and Pandav, 2012; Long *et al.*, 2011; Negroes *et al.*, 2010). Information collected from landowner questionnaires (e.g. fence type, property size, land use, attitude towards brown hyaenas) and habitat assessments were quantified and inputted as covariates. I divided large raw values within these data sets such as property sizes by a constant to reduce the range of the data (Nijhawan, 2010). Categorical covariates were created utilising 0s and 1s for descriptive factors such as habitat (following Harihar and Pandav, 2012).

Multicollinearity can disrupt clear outcomes in regards to detection probabilities (MacKenzie and Bailey, 2004). I tested relationships between each pair of covariates for multicollinearity in R v 3.2.3 (R Development Core Team, 2016) using the Spearman's Rank Correlation test, the Wilcoxon rank-sum test, the Kruskal-Wallis test, and the chi-squared test. Test selection was dependent upon which combination of data was being tested and the type of data (numerical: continuous or discrete, or categorical). Any pairwise correlation coefficients with Rho exceeding 0.6 in the same

model in the Spearman's Rank Correlation tests (following Gerber *et al.*, 2012) and any significant models ($p \leq 0.05$) in all other tests were considered correlated. I excluded one covariate from each pair if a significant relationship was found. For example, BAI data correlated closely with corresponding RAI values (e.g.: BAI of Antelope and RAI of Antelope; Spearman's Rank Correlation: $Rho = 0.866$, $S = 109.7$, $p < 0.001$), therefore either the RAI or BAI covariate was excluded from the occupancy analysis.

This study did not include survey covariates because methods were fixed across all sites. I ran single-season single-species occupancy analysis to determine true brown hyaena occupancy (Ψ) and probability of detection (p). I ran intercept models that tested a standardised Ψ and p across time, and sites with no covariate effects. The constant (null reference) model, $\Psi(.)p(.)$, assumes that brown hyaena site use and detection probably was constant across sites and was used as a reference. Then all covariates were tested against Ψ with p as a constant.

I tested the significance of site covariates on Ψ and p using logistical regression analysis. All models were fitted using logistic link and parametrically bootstrapped at 10,000. Bootstraps at or exceeding 10,000 are recommended for analysis with large capture occasions (>10) to correctly address the distribution of the test statistic (MacKenzie and Bailey, 2004).

Models were compared using maximum likelihood methods to rank the most parsimonious models and define the confidence set. I used Akaike's information criterion (AIC) to rank models and higher-ranking models received the lowest AIC values (Burnham and Anderson, 1998). A confidence set of top ranking models was selected by checking if the models made biological sense, had a low AIC score, and had a good fit of data (Symonds and Moussalli, 2011). Within the confidence set there is often little differentiation between the top models as they are frequently variations of the same covariate based themes (Symonds and Moussalli, 2011). Therefore, I retained models with the highest ΔAIC values and disregarded the more complex and lower ranking models (Richards, 2008). The difference between the best model (which has a ΔAIC of 0) and each subsequent model is calculated using ΔAIC (Burnham and Anderson, 2004). AIC weight provided a probability that a model is the best by

combining all models in the set to sum one (Symonds and Moussalli, 2011). Models with a ΔAIC of <2 were classed as equivalent top models (following Burnham and Anderson, 2004; Li *et al.*, 2010; Shake *et al.*, 2012; Sunarto *et al.*, 2012; Thorn *et al.*, 2009). Models with a ΔAIC between 2 and 7 offer some support (Burnham *et al.*, 2011) and models with a ΔAIC greater than 10 offer no support (Burnham and Anderson, 2004). The confidence set was comprised of models with ΔAIC of 7 or lower.

AIC assesses models in relation to each other but does not indicate if the entire model collection is poor overall (Burnham *et al.*, 2011; MacKenzie and Bailey, 2004). Therefore, I conducted goodness of fit tests on each independent model to ensure that I retained ideal models (Burnham and Anderson, 2004). Pearson chi-squared tests assessed goodness of fit by measuring the distribution of observed data within each model to the worst model (MacKenzie and Bailey, 2004). A poor fit can occur in situations when an unexpectedly high number of sites detect an animal or if an unmeasured site characteristic is affecting occupancy (MacKenzie and Bailey, 2004). When the data was initially run almost all models showed poor fitness and severe overdispersion. A model is overdispersed when the sampling variance is greater than the theoretical variance (Burnham and Anderson, 1998). The overdispersion parameter $c\text{-hat}$, which indicates a model's fitness, should be close to one in a well-dispersed model (Nijhawan, 2010; Steinmetz *et al.*, 2013). Many of the initial models' $c\text{-hat}$ values were around 2.5. Additionally, the standard error estimates were not statistically significant (<0.05), the confidence interval included zero, and the sign (+ or -) of the covariate estimate did not always agree with existing information on trends within the species' ecology, which all pointed to poor fitness (Nijhawan, 2010). I hypothesised that sampling results from station 18 were affecting this misalignment. Camera station 18 was unknowingly placed next to a brown hyaena den causing this station to record considerably greater brown hyaena activity than any other location (21.7% of all brown hyaena capture events were from station 18). I removed station 18 from the final data set and consequently all confidence set models achieved normal dispersion and goodness of fit.

I conducted model averaging to further differentiate between similar ranking top models (Burnham and Anderson, 2004; Symonds and Moussalli, 2011) because no

model emerged as the top model ($w > 0.90$) (Burnham and Anderson, 2002; Linkie *et al.*, 2007b). Following Linkie *et al.* (2007b), Constant (2014), and Thorn *et al.* (2011a), model averaged estimates of Ψ and p were determined using equations described by Burnham and Anderson (2002). Model averaging was conducted using the model-averaged estimates function in PRESENCE v 10.2 (MacKenzie, 2016).

I used model averaged estimates of Ψ at each station to estimate true occupancy. The wide spacing of the cameras which met or exceeded a brown hyaena's home range enabled estimates of true occupancy in contrast to more closely nested surveys which estimate how intensely the habitat is used (Karanth *et al.*, 2011a). I tested model averaged values of occupancy across areas and habitat types for significance using R v 3.2.3 (R Development Core Team, 2016).

5.3.3.3. Spatially explicit capture recapture

I estimated density using a smaller camera trapping array with different set up requirements than the occupancy analysis (section 5.3.1.2). The 2014 and 2015 surveys were analysed separately using Bayesian spatially explicit capture recapture models (Royle *et al.*, 2009) within the R package, SPACECAP v 1.1.0 (Gopalaswamy *et al.*, 2012). Analysis within SPACECAP requires a capture history file, a trap deployment file, and a potential home range centres file for each sampling period (Blancoa *et al.*, 2013). Capture histories are a record of the individual hyaenas sighted at each camera trapping location on each of the sampling occasions. I defined a sampling occasion as a 24-hour period from 12:00 pm to 12:00 pm. I selected a sampling occasion which incorporated the full duration of the night to avoid the 'midnight problem' whereby an animal photographed on both sides of midnight is recorded as separate captures (Jordan *et al.*, 2011, p. 269). This is an appropriate approach for exclusively nocturnal species like the brown hyaena (Foster and Harmsen, 2012).

The trap deployment file was inputted into SPACECAP to indicate sampling occasions when specific camera stations were not functioning and therefore did not have the possibility of capturing a brown hyaena (Gopalaswamy *et al.*, 2014). In the binary

matrix, a 1 indicated sampling occasions when one or both cameras were active. If both cameras at the station were not functioning on a specific sampling occasion, a 0 was placed in the matrix (Gopalaswamy *et al.*, 2014).

I generated the potential home range centres file using QGIS v 2.6 (Quantum GIS Development Team, 2014) and RStudio v 0.99.489 (RStudio, 2015). Not all animals photographed live exclusively within the camera trapping grid; the home ranges of many hyaenas will straddle the boundary and this must be considered in density estimation (O'Brien, 2011). The home range centres file estimates the entire area where all photographed brown hyaenas could live. In RStudio, I added a buffer based on estimated home range size to the *Universal Transverse Mercator* (UTM) coordinates of every camera station that photographed a brown hyaena on the assumption that any animals outside the buffer should not be photographed. Brown hyaenas in the western Soutpansberg Mountains have large home ranges (Chapter 6). Two of the brown hyaenas photographed in the camera trapping survey were previously collared individuals making home range data from the collars very applicable in determining suitable buffer size for the home range centres. I tested buffer sizes to determine where density estimates plateaued. A buffer of 30 km was applied with a home range centre spacing of 500 m to create the state-space. The grid produced incorporates all potential home range centres, however some of the areas included may not be suitable brown hyaena habitats. Unacceptable areas include buildings, communities, and watercourses. Non-habitat areas (=0) and potential habitats (=1) were identified in the home range centres matrix.

The SECR analysis employed the Bernoulli encounter process, a half normal detection function, and a present trap response. In 2014, Markov-Chain Monte Carlo iterations were set at 100,000 with a burn-in period of 20,000, a thinning rate of 1, and a 300 data augmentation value. In 2015, Markov-Chain Monte Carlo iterations were set at 100,000 with a burn-in period of 40,000, a thinning rate of 1, and a 380 data augmentation value. I confirmed convergence visually by examining the Geweke diagnostics and output plots following Gopalaswamy *et al.* (2014).

5.3.3.4. Estimating brown hyaena density in the occupancy survey area

SECR using the programme SPACECAP is one of the most accurate methodologies to estimate density (Blancoa *et al.*, 2013; Gopalaswamy *et al.*, 2012; Noss *et al.*, 2012), however due to financial and strategic limitations of camera trapping, the SECR density estimate only provides density information pertaining to the western Soutpansberg Mountains. To overcome this limitation, I extrapolated the 2014 SECR density estimate to approximate population within the larger occupancy survey area, following methods used by Thorn *et al.* (2009). I utilised the density estimate from 2014 because the data collection timeframe overlapped with the period when I conducted the occupancy survey. I determined the proportional area of the 2014 SECR camera trapping grid in relation to the brown hyaena occupied camera trapping grid for occupancy. I multiplied the density of brown hyaenas estimated in the western Soutpansberg Mountains in 2014 by this proportion to estimate the number of hyaenas within the occupancy survey area.

5.4. Results

5.4.1. Occupancy and factors affecting occupancy and detection

After removing station 18, the occupancy survey spanned 17 camera station locations and totaled 1,118 camera trapping days (Table 5.3). A total of 51 non-domesticated mammal species were recorded (Appendix 6); 20 of these were carnivores. Twelve out of 17 stations (71%) photographed brown hyaenas and brown hyaena captures accounted for 1.3% of all total captures.

Table 5.3 Summarised sampling effort from the occupancy camera trapping survey conducted between June 23 and August 27, 2014 in and around the Soutpansberg Mountains.

	N	% of total
Camera trap stations	17	-
Potential trapping days	1,122	-
Days when a station was not functioning	4	-
Total camera trapping days	1,118	-
Mean trapping days per station	65.76	-
Number of images taken	47,438	100
Number of usable images*	38,469	81.1
Independent capture events	3,617	100
Number of mammal species**	51	-
Mammal capture events**	1,999	55.3
Number of predator species	20	39.2
Predator capture events	791	21.9
Number of brown hyaena images	232	0.6
Brown hyaena capture events	47	1.3
Number of stations which photographed brown hyaenas	12	70.6
Number of bird species	18	-
Bird capture events	243	6.7
Domestic capture events***	193	5.3
Human capture events	669	18.5
Vehicle capture events	451	12.5

*Excludes blank frames (n = 8857) and images of unidentifiable species (n = 112).

** Excludes domestic animals and humans.

*** Cows, donkeys, goats, and sheep.

After excluding models that tested positive for multicollinearity, environmental and anthropogenic covariates were considered against occupancy and probability of detection to investigate hypotheses in Table 5.1. Eleven models had $\Delta AIC < 7$ and these were included in the candidate set (Table 5.4).

Table 5.4 Summary of top-ranked single-season single-species occupancy models for brown hyaena. AIC: Akaike's information criterion, Δ AIC: difference in AIC between each model and the top ranking model, w : AIC weight, K : number of parameters, $-2 \cdot \text{ll}$: twice the negative log-likelihood (the deviance). A positive or negative beta estimate (β) indicates the same directional effect on dependent covariates. The covariate affects occupancy in lightly shaded models and the covariate affects probability of detection in non-shaded models. The model $\text{psi}(\cdot), \text{p}(\cdot)$ is the null model where all sites have a constant Ψ and p estimate (Nijhawan, 2010). The null model is denoted with the darkest shading.

Model	AIC	Δ AIC	w	K	$-2 \cdot \text{ll}$	β estimates (\pm S.E.)
$\text{psi}(\cdot), \text{p}(\text{acceptancelevelforbh})$	173.5	0	0.4807	4	165.5	*
$\text{psi}(\text{RAIhuman}), \text{p}(\cdot)$	175.79	2.29	0.153	3	169.79	-2.056273 (1.23737)
$\text{psi}(\text{size of property}), \text{p}(\cdot)$	177.25	3.75	0.0737	3	171.25	-0.324298 (0.260639)
$\text{psi}(\cdot), \text{p}(\text{size of property})$	177.73	4.23	0.058	3	171.73	0.364396 (0.158185)
$\text{psi}(\text{game fences}), \text{p}(\cdot)$	177.77	4.27	0.0568	3	171.77	2.991745 (1.976065)
$\text{psi}(\text{habitatthickness}), \text{p}(\cdot)$	178.52	5.02	0.0391	4	170.52	**
$\text{psi}(\cdot), \text{p}(\text{kill bh})$	178.59	5.09	0.0377	3	172.59	1.301471 (0.646908)
$\text{psi}(\cdot), \text{p}(\text{BAIlargecarnivores})$	179.29	5.79	0.0266	3	173.29	0.510836 (0.279926)
$\text{psi}(\cdot), \text{p}(\text{cattle fences})$	179.4	5.9	0.0252	3	173.4	0.786101 (0.443874)
$\text{psi}(\cdot), \text{p}(\text{game fences})$	180.14	6.64	0.0174	3	174.14	-0.702858 (0.443804)
$\text{psi}(\text{RAIcarnivores}), \text{p}(\cdot)$	180.18	6.68	0.017	3	174.18	-0.874449 (0.617843)
$\text{psi}(\cdot), \text{p}(\cdot)$	180.46	6.96	0.0148	2	176.46	0.994584 (0.584761)

*Likes brown hyaenas: $\beta = 0.3769 (\pm 0.0605)$, Dislikes brown hyaenas: $\beta = 0 (\pm 0)$, Neutral towards brown hyaenas: $\beta = 0.146 (\pm 0.0459)$

** Open: $\beta = 0.8293 (\pm 0.1323)$, Mixed: $\beta = 1 (\pm 0)$, Closed: $\beta = 0.2577 (\pm 0.2232)$

The global model ($\text{psi}(\cdot), p(\text{acceptancelevelforbh})$) fit the data well (probability of test statistic \geq observed from 10,000 parametric bootstraps = 0.5747). C-hat is estimated at 0.8095 and the confidence interval does not overlap 0 (C.I = 0.25832 and 0.49548).

Models with a constant psi generally rank similarly to psi (covariate) models. This indicates that the influence of environmental covariates on detection probability is equally important to its influence on occupancy.

Brown hyaena occupancy and probability of detection are most strongly influenced by covariates associated with human impact. Human RAI has the greatest influence on occupancy; where human activity is higher, occupancy is lower. Probability of detection is higher on properties where the landowners like brown hyaenas. Brown hyaena detection is higher on properties where the landowner admits to killing them. Human-induced land management techniques including property size and fencing type impact upon occupancy and detection. Brown hyaena occupancy is lower on larger properties yet probability of detection is higher.

There is a significant difference in brown hyaena occupancy at stations with different fence types (Kruskal-Wallis: chi squared = 7.85, df = 2, p = 0.019) (Figure 5.6). Properties with game fences (generally game farms) have higher brown hyaena occupancy. The presence of cattle fences makes it easier to detect hyaenas. The opposite relationship is found with game fences.

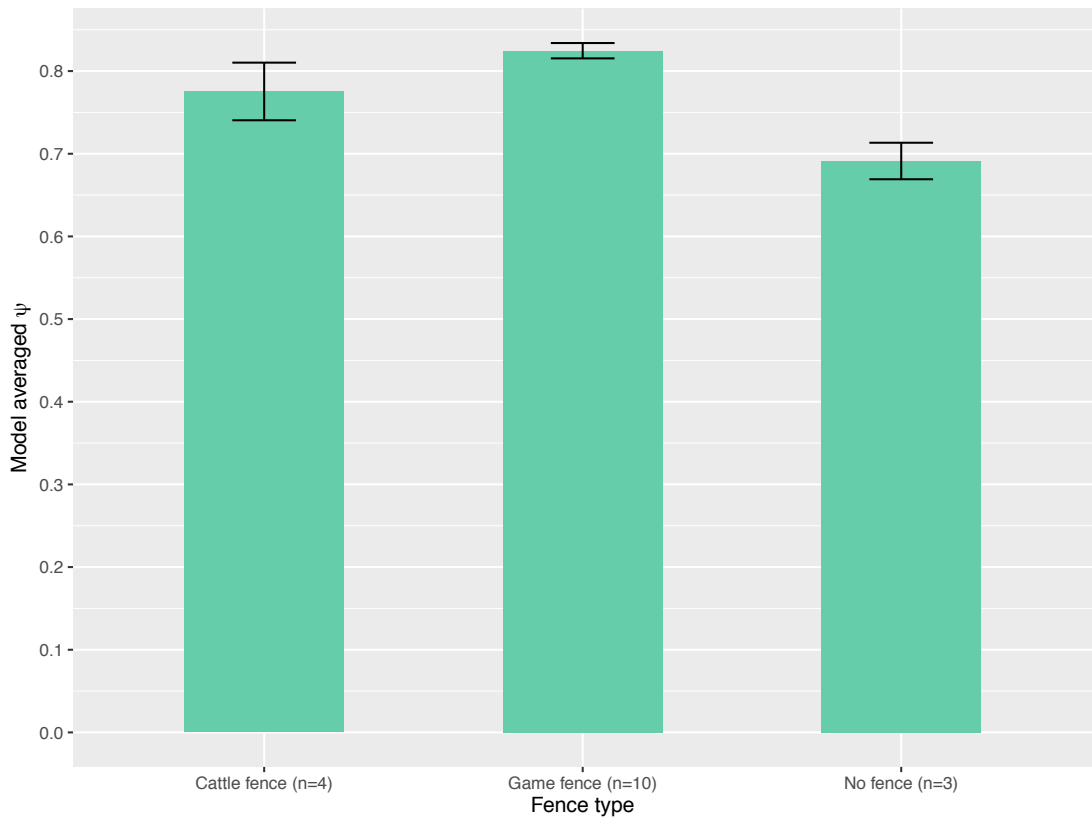


Figure 5.6 Model averaged occupancy per fence type in and around the Soutpansberg Mountains. n = the number of camera stations in each category. Error bars represent standard error.

Prey availability and species diversity does not have a strong impact upon occupancy and probability of detection. However, properties with game fences have significantly higher RAI of medium prey (Wilcoxon rank-sum test: $W = 13$, $df = 1$, $p = 0.033$), BAI of antelope (Wilcoxon rank-sum test: $W = 4$, $df = 1$, $p = 0.003$), and RAI of large prey (Wilcoxon rank-sum test: $W = 11$, $df = 1$, $p = 0.022$). Since a model testing occupancy with game fences ranks highly ($\Delta AIC = 4.27$), this suggests that the availability of medium and large prey species is important to hyaena occupancy.

Interspecies competition has a moderate effect on brown hyaena occupancy ($\psi(\text{RAIcarnivores}), p(.)$ $\Delta AIC = 6.68$) and detection probability ($\psi(.), p(\text{BAIlargecarnivores})$ $\Delta AIC = 5.79$). A higher relative abundance of all carnivores (excluding brown hyaena) lowers brown hyaena occupancy. In areas where there is a high biomass of large carnivores, brown hyaena detection is easier.

Habitat influences brown hyaena occupancy ($\Delta AIC = 5.02$) Occupancy is highest in areas with a mix of woodland/grassland and lowest in mostly closed/woodland areas. Habitat does not affect the probability of detection. Habitat is also significantly correlated with occupancy (Kruskal-Wallis: chi squared = 8.16, df = 2, p = 0.017) (Figure 5.7).

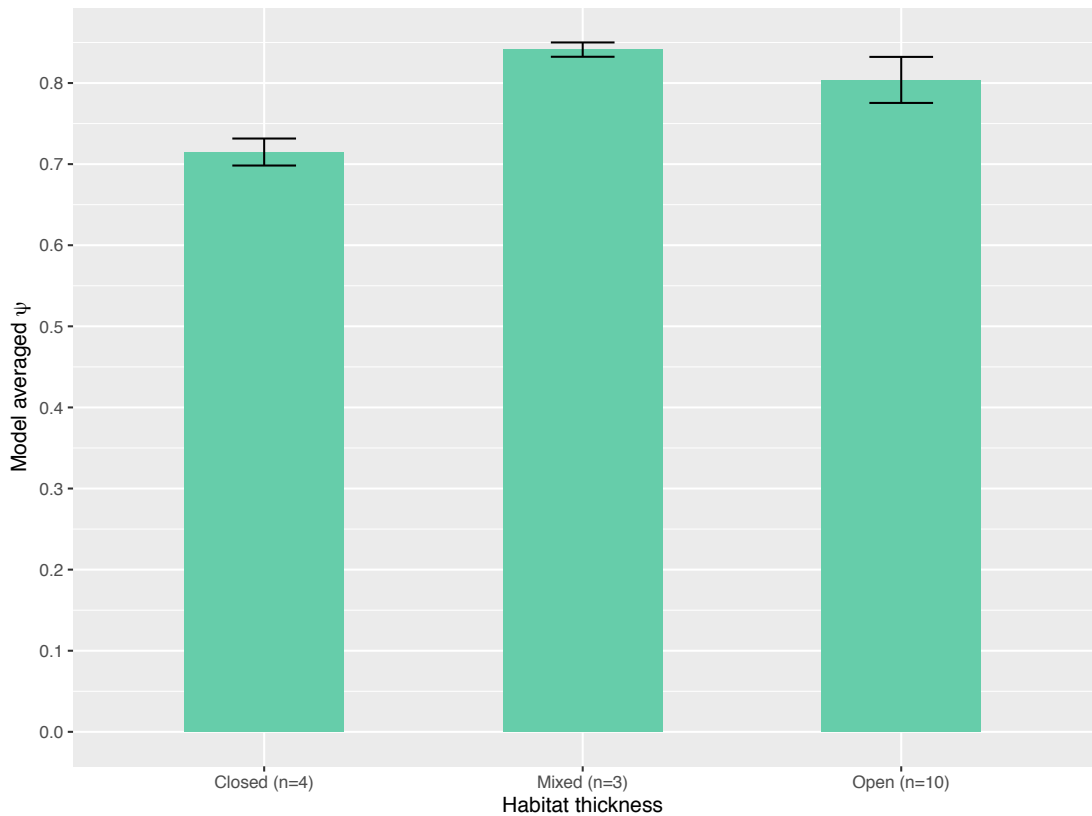


Figure 5.7 Model averaged occupancy per habitat thickness in and around the Soutpansberg Mountains. Habitat thickness is categorised into Open (mostly open/grassland), Mixed (mix of woodland/grassland), and Closed (mostly closed/woodland). n = the number of camera stations in each category. Error bars represent standard error.

Camera stations occurred into the following land use types (LUTs): Game farming only (n = 5), Game/livestock farming (n = 5), Game/livestock/agricultural farming (n = 2), Livestock farming only (n = 1), Livestock/agricultural farming (n = 3), and Unmanaged (n = 1). There is no significant difference in occupancy (Kruskal-Wallis: chi squared = 5.48, df = 5, p = 0.361) or probability of detection (Kruskal-Wallis: chi squared = 2.872, df = 5, p = 0.72) across LUTs.

There is no significant difference in occupancy (Kruskal-Wallis: chi squared = 1.816, df = 2, $p = 0.403$) or probability of detection (Kruskal-Wallis: chi squared = 0.404, df = 2, $p = 0.817$) between the Soutpansberg Mountains, Limpopo Valley, and the lowveld.

As no models, including the global model, emerged as the top model ($w > 0.90$) model averaging was used to compute final values for Ψ and p (following Linkie *et al.*, 2007b) (Table 5.5).

Table 5.5 Model averaged estimates of Ψ and p for camera stations in and around the Soutpansberg Mountains.

Camera station	Model averaged Ψ	Standard error	Model averaged p	Standard error
1	0.8431	0.2071	0.3164	0.0967
2	0.7843	0.4506	0.3119	0.1103
3	0.8457	0.2046	0.2039	0.0802
4	0.8236	0.2674	0.3343	0.1466
5	0.7803	0.716	0.2582	0.7161
6	0.8411	0.2076	0.2056	0.0792
7	0.6709	0.6134	0.1737	0.546
8	0.8424	0.2014	0.317	0.1005
9	0.8512	0.2279	0.2018	0.0797
11	0.8054	0.3045	0.3495	0.1579
12	0.8488	0.228	0.2112	0.0915
13	0.786	0.478	0.207	0.0859
14	0.6528	0.8803	0.3128	0.1213
15	0.7293	1.009	0.2509	0.6364
16	0.8116	0.3178	0.2123	0.1374
17	0.8135	0.3106	0.3196	0.1132
19	0.6916	0.7865	0.2029	0.1138
All sites	0.7895	0.0649 (S.D.)	0.2582	0.0595 (S.D.)

The naïve occupancy level is estimated at 0.705823. Model averaging predicts that brown hyaenas occupied ~79% of the area surveyed across the 66-day sampling period ($\Psi = 0.7895$, S.D. = 0.0649) (Table 5.5). Of the 4,974.62 km² sampled (size of grid after station 18 was excluded), an area of 3,927.62 km² is considered potential brown

hyaena habitat according to the true occupancy estimate. The occupancy level exceeds the naïve occupancy estimate by 8%. The model averaged probability of detection for brown hyaenas is 0.2582 (S.D. = 0.0595) (Table 5.5).

5.1.1. Estimate of brown hyaena density in the western Soutpansberg Mountains

In 2014, 22 brown hyaenas were photographed in the 220 km² sampling area. In 2015, 22 brown hyaenas were identified in a 200 km² sampling area. The sampling areas were similar with a 90% overlap of station locations replicated both years. Seventeen hyaenas (77%) were sighted in both years indicating that there was a 23% turnover rate.

In 2014, brown hyaena density was 2.56 per 100 km² (95% confidence interval = 1.14). In 2015, brown hyaena density was 3.63 per 100 km² (95% confidence interval = 1.84) (Table 5.6).

Table 5.6 SPACECAP results from the 2014 and 2015 sampling periods conducted to estimate brown hyaena density in the western Soutpansberg Mountains.

Sampling period	Effective posterior sample size	Geweke z score for sigma	Geweke z score for lam0	Geweke z score for beta	Geweke z score for psi	Geweke z score for Nsuper	Bayesian p-value
2014	1106.1106	-0.586	-1.4546	0.2901	0.3561	0.3601	0.68145
2015	633.058	0.5808	-0.805	1.2673	-0.743	-0.7777	0.6179833

Sampling period	Density - posterior mean (animals per 100 km ²)	Density - posterior SD	Density - 95% lower HPD (animals per 1 km ²)	Density - 95% upper HPD (animals per 1 km ²)	Lower density estimate (animals per 100 km ²)	Upper density estimate (animals per 100 km ²)	Average difference between density extremes
2014	2.56	0.00594	0.0143	0.037	1.43	3.7	1.835
2015	3.63	0.00952	0.0176	0.0543	1.76	5.43	1.135

5.1.2. Estimate of brown hyaena population in the occupancy survey area

There was an estimated population of 45.7 brown hyaenas within the 4,974.62 km² occupancy survey area in 2014.

5.2. Discussion

5.2.1. Occupancy outcomes

Brown hyaenas are present across the majority of the sample area and presumably a large tract of northern Limpopo Province. This is in line with findings from other South African studies, which also detected widespread brown hyaena occupancy (Richmond-Coggan, 2014; Thorn *et al.*, 2011a). This outcome is positive for brown hyaena conservation as it offers additional support that the species' can survive in non-protected areas and in human-manipulated landscapes (Kent and Hill, 2013; Thorn *et al.*, 2011a).

Brown hyaena presence exceeds the naïve occupancy by 8%, indicating that brown hyaenas occupy at least one of the sites where the species was not detected during the sampling period. I am confident that this is the case because two sites that did not detect the species during the sampling period (June – August 2014) photographed brown hyaenas during the pilot study (April – June 2014). As a secretive species, brown hyaenas may occupy spaces largely unbeknownst to people (Kuhn, 2014). The camera station which yielded the highest photographic capture rate for brown hyaenas was on a livestock farm, where the landowner assured me that no brown hyaenas had lived for the past 10 years. This indicates that brown hyaenas can occupy land used for livestock farming without coming into conflict with humans and it matches sentiments about coexistence expressed by some livestock farmers (Chapter 3).

The candidate set enables the rejection or acceptance the original hypotheses (Table 5.1). Covariates associated with human impact have the greatest influence on brown

hyaena occupancy, with brown hyaenas avoiding areas of high human activity. This finding, which confirms hypothesis 5.3, is not surprising considering the variety of anthropogenic threats that I identified across the study area during interviews (Chapter 3 and 4). From my GPS collaring data, brown hyaenas regularly move across a number of different land use types (Chapter 6). As the interview results demonstrate, some properties offer a haven for predators and others poison carcasses for predators to consume (Chapter 3 and 4). Brown hyaenas' avoidance of areas with a high human RAI is understandable because very few properties in the study area are large enough to encompass the entire home range of a brown hyaena and guarantee their safety. These results correspond with species-specific findings that brown hyaena occupancy and relative abundance is higher in protected areas than unprotected areas (Richmond-Coggan, 2014; Thorn *et al.*, 2011a) and human avoidance trends found in other hyaenid species. Striped hyaena occupancy increases in rugged areas free of human activity and in areas that have a greater distance from human habitation in a protected area, Ranthambhore Tiger Reserve, Rajasthan (Singh *et al.*, 2014).

Brown hyaena occupancy is higher on properties with game fences (generally game farms), rejecting hypothesis 5.6. Human activity is often lower on game farms than on livestock and agricultural farms. Game farms can also offer higher prey abundance and reliable scavenging opportunities through vulture restaurants or animals wounded in hunts. Game farms have a strong positive effect on brown hyaena occupancy in North West Province (Thorn *et al.*, 2011a). It is assumed that anthropogenic threats are lower on game farms than other land use types, explaining this trend (Thorn *et al.*, 2011a). Some studies detected high brown hyaena occupancy on agricultural land (Thorn *et al.*, 2011a; Thorn *et al.*, 2011b) and on livestock farms (Kent and Hill, 2013). There are many livestock farms in the survey area, and properties with cattle fences have the second highest occupancy.

Brown hyaena occupancy is lower on larger properties while their probability of detection is higher. This rejects hypothesis 5.5. Larger properties have a lower density of prey species than smaller properties where the prey is more well-stocked within a smaller area. Less human threats and more open habitats on large game farms may explain the greater detectability there.

Although a previous study found that positive attitudes towards carnivores have a positive impact on brown hyaena occupancy (Thorn *et al.*, 2011a), I did not detect a similar trend. Attitudes and behaviours towards brown hyaenas did, however, affect their probability of detection. On properties where the landowner has a positive attitude towards brown hyaenas, hyaenas are more likely to be detected. This links to conclusions presented in Chapter 3, that positive attitudes are more common amongst respondents who had greater knowledge of the species. This often arises from real experiences with the animal such as visual sightings. Conversely, landowners who admit to killing brown hyaenas are also more likely to detect them on their land, indicating that high visibility can produce varied outcomes. Animals might be killed on these properties because they cause problems for livestock and are therefore less evasive. A farmer's response to a more visible animal may be dependent upon other complex factors such as a legacy of killing predators on their land, education levels, problems with other predators, and financial stability (Chapter 4).

High tiger and leopard occupancy is associated with high prey availability (Steinmetz *et al.*, 2013). High prey activity (calculated as RAI) increases leopard occupancy in and around the Blouberg Mountain Range, South Africa (Constant, 2014). However, there is no correlation between total RAI or BAI and brown hyaena occupancy, indicating that prey abundance does not have a very strong influence on occupancy in this study and rejecting hypothesis 5.1. Similarly, prey abundance is not a significant driver of brown hyaena occupancy in Pilanesberg National Park (Thorn *et al.*, 2009). This is due to the importance of scavenging for brown hyaenas. A model testing species richness against occupancy had a low weighting ($\Delta AIC = 8.61$) and was not included in the candidate set. This is another indicator of the brown hyaena's adaptive and varied diet, which is typical of a scavenger. These findings are indicative that brown hyaenas in this region are likely to predominantly scavenge rather than hunt.

I calculated BAI values by incorporating weight ranges of animals and group size. High BAI values in antelope species and medium sized prey have a positive effect on brown hyaena occupancy. This correlates with findings from dietary studies showing that brown hyaenas prefer large (Burgener and Gusset, 2003; Maddock, 1993; Mills, 1982a; Owens and Owens, 1978; van der Merwe *et al.*, 2009; Yarnell *et al.*, 2013) or medium

sized prey (Maddock, 1993). Alternatively, this result may reflect a greater number of antelopes and medium sized prey on game farms than on other land use types.

In areas with higher overall carnivore abundance, brown hyaena occupancy is lower, rejecting part of hypothesis 5.2. Considering the high dietary overlap between brown hyaenas and leopards (Stein *et al.*, 2013), this result is unexpected. Greater carnivore abundance might have increased scavenging competition by other species. A negative association between tiger and leopard occupancy indicates spatial avoidance (Steinmetz *et al.*, 2013). Puma (*Puma concolor*) occurrence is negatively correlated with the presence of jaguars but only at a low level, suggesting some spatial avoidance (Sollmann *et al.*, 2012). Jaguars are likely to be dominant and this is supported by their larger size (Sollmann *et al.*, 2012). The brown hyaena's smaller stature in comparison to spotted hyaenas and leopards may provoke a similar effect. Alternatively or additionally, heated animosity towards leopards and spotted hyaenas (Chapter 3) may cause landowners and managers to conduct retaliatory behaviours such as poisoning, affecting the entire large carnivore guild, which in turn may lower brown hyaena occupancy.

The probability of detecting brown hyaenas increases in areas with greater abundances of large carnivores (leopards, wild dogs, and spotted hyaenas) in agreement with hypothesis 5.2. This may be because brown hyaenas move more when other large carnivores are present. In the Kgalagadi Transfrontier National Park, brown hyaenas often move away from an area when they detect spotted hyaena presence (Mills, 1990).

Altitude does not affect brown hyaena occupancy or probability of detection. This finding does not support hypothesis 5.8. Habitat thickness influences occupancy, which rejects hypothesis 5.7. Mountainous bushveld is a favoured habitat for brown hyaenas (Mills and Hofer, 1998; Skinner, 1976) yet in line with Thorn *et al.* (2009), elevation and mountainous areas do not yield higher occupancy levels. Brown hyaenas prefer areas with a mixture of open and closed habitats and open areas to areas with closed habitat. Areas of mixed habitat offer some shelter from humans yet also

provide access to open areas, which facilitate the large foraging distances brown hyaenas cover nightly.

All covariates tested fall into one of four broad categories: human impact; prey size and abundance; interspecific competition; and habitat and environmental factors. These factors link with the fourteen key factors, which Winterbach *et al.* (2013) identified as affecting large African carnivore conservation. The covariates and their associated categories do not act independently. Higher occupancy levels may be attributed to several interrelated aspects; therefore brown hyaena conservation strategies require a varied approach, which considers a wide array of conditions.

Occupancy has recently been applied to model, predict, and understand human-wildlife conflict. Factors affecting crop raiding behaviour by Asian elephants (*Elephas maximus*) were modeled and the information collected has been used to predict future conflict and design management practices (Goswami *et al.*, 2015). This might be a useful approach to brown hyaena conservation if more detailed social science data and the location of farms or communities where damage-causing animal permits are issued are incorporated into occupancy models.

5.2.2. Density estimates

Brown hyaena density in the western Soutpansberg Mountains was estimated at 2.56 per 100 km² (± 1.14) in 2014 and 3.63 per 100 km² (± 1.84) in 2015. Although the 2015 estimate is higher than the previous year's, due to overlapping confidence intervals, there is unlikely to be a significant increase between the periods. These represent some of the first brown hyaena density estimations in a montane environment. The results are comparable to density estimates from Pilanesberg National Park (2.8 per 100 km² (Thorn *et al.*, 2009)) and Mankwe Wildlife Reserve (2 – 4 per 100 km² (Yarnell *et al.*, 2013)) in North West Province; the only other semi-mountainous areas previously surveyed for brown hyaena density. Brown hyaena density in the Soutpansberg Mountains is higher than estimates from desert environments in the Kgalagadi Transfrontier National Park, coastal areas in Namibia, and the Makgadikgadi

National Park and surrounding area, Botswana (Table 5.2) (Maude, 2005; Mills, 1990; Wiesel, 2006). With greater and more reliable food availability and regular water sources, this result is expected. Brown hyaena density in the Soutpansberg Mountains is similar to estimates from Ghanzi, Botswana (Boast and Houser, 2012; Kent and Hill, 2013), one of the only other sites previously surveyed outside of a protected area.

Areas with the highest recorded brown hyaena densities host high densities of apex predators (Thorn *et al.*, 2009; Welch, 2014; Yarnell *et al.*, 2013), offering plentiful scavenging opportunities. A similar scenario exists in northern Limpopo Province. In 2008, the Soutpansberg Mountains hosted the highest reported leopard density outside of state-protected areas in sub-Saharan Africa (Chase Grey *et al.*, 2013). The success of this population was attributed to high prey densities and low levels of livestock farming (Chase Grey *et al.*, 2013). The leopard population in the western Soutpansberg Mountains has declined by 66% between 2008 (Chase Grey *et al.*, 2013) and 2015 (Williams *et al.*, in review-b). Human persecution, especially through illegal snaring and poisoning, is suspected to be responsible for high leopard mortality (Williams *et al.*, in review-b).

The leopard population's decline might affect brown hyaena numbers either positively or negatively. In many systems, a decline in large carnivores may create a surge in smaller carnivore numbers. Food sources become more abundant and interspecies competition lowers through mesopredator release effect (Crooks and Soulé, 1999). Density is affected by food availability and quality (Mills, 1982a; Mills, 1984) and with fewer leopards in the Soutpansberg Mountains, there may be more food available for brown hyaenas. Although brown hyaenas are also susceptible to snaring and poisoning, in the brown hyaena population a mesopredator release effect could compensate for any human-induced population declines. Alternatively, leopard decline could provoke a decline in the brown hyaena population, due to the brown hyaena's reliance upon apex predators for scavenging (Owens and Owens, 1978; Slater and Muller, 2014) or stimulate a greater prevalence in hunting behaviour by brown hyaenas (van der Merwe *et al.*, 2009). Thicker habitats in mountainous areas provide an ideal hunting ground for ambush predators like leopards (Balme *et al.*, 2007). Although brown hyaenas benefit from concealment in long grasses or bushes to

surprise small prey, they are not especially stealthy or successful hunters (Owens and Owens, 1978). Subsequently as scavenging opportunities in the Soutpansberg fall, mountain-dwelling brown hyaenas may need to widen their foraging areas or relocate to more dangerous areas off the mountain. Continual population monitoring is recommended.

5.2.3. Population estimate in the occupancy survey area

Within the occupancy survey area the brown hyaena population is estimated at 45.7 individuals. This estimate is based on the assumption that brown hyaena density across the entire study site is the same as the 2014 SECR density estimate. Carnivore densities can vary greatly due to differing resource availability, habitat variation, and risk levels across altitudes and LUTs (Karanth *et al.*, 2004), therefore this population estimate should be treated with some caution as it represents a rough estimate (Foster and Harmsen, 2012).

The estimated population within the occupancy study site represents 4.538% of the national population of brown hyaenas estimated by Thorn (2009) and 4.57% of the population estimated within the Transvaal by Mills and Hofer (1998). As expressed in section 1.4, information on the number of brown hyaenas within South Africa is conflicting when compared to estimates pertaining exclusively to the Transvaal region, thus explaining the similarity in the percentages. However on either scale, the number of brown hyaena resident within the study site is sufficiently high enough to be of significant importance to the conservation of the species both regionally and nationally.

If the annual number of hyaenas killed by people could be accurately established within the study area or a proportion of the study area, this information could be applied to the 2014 population estimate and information on births, deaths, immigration, and emmigration to predict long-term trends. Although I acquired some data through interviews on the number of brown hyaenas killed by anthropogenic threats in the area, this was not sufficiently reliable or thorough to predict trends. I could not quantify all illegal anthropogenic mortalities in the study area as snaring

losses are very difficult to accurately determine (Madhusudan and Karanth, 2002). Future research on brown hyaena populations and densities should attempt to quantify legal and illegal annual losses from the onset to predict population trends.

5.3. Summary

Brown hyaena occupancy across a wide area which includes the Soutpansberg Mountains and flatlands to the north and south, is estimated to cover ~79% of the area surveyed ($\Psi = 0.7895$, S.D. = 0.0649). Factors which have a positive influence on brown hyaena occupancy include mixed and open habitat thickness, properties with game fences, an abundance of medium sized prey, and, most importantly, low human activity. Areas meeting these criteria are important for brown hyaena conservation outside of protected areas. However, these areas can still harbour high risks for hyaenas from snaring, poisoning, and other anthropogenic sources despite low human activity. Therefore, because of the large home ranges of brown hyaenas and their ability to occupy a wide variety of habitats and land use types, it is important to preserve all potential areas of occupancy in northern Limpopo Province. The Soutpansberg Mountains, which is a less ideal region for brown hyaena in terms of habitat thickness, may act as a conservation refuge from human-induced mortality.

The occupancy results suggest that variables such as human activity and habitat thickness affect brown hyaena occupancy. It is expected that hyaena density may vary in relation to the presence or absence of these factors between the Soutpansberg Mountains, the Limpopo Valley, and the lowveld. SECR density surveys across these areas are recommended.

Brown hyaena density in the western Soutpansberg Mountains was estimated at 2.56 per 100 km² (± 1.14) in 2014 and 3.63 per 100 km² (± 1.84) in 2015. These estimates are comparable to other studies in similar habitats and in non-protected areas. Although this is reassuring, with a substantial change in the leopard population underway, the brown hyaena population may shift over the next few years. Continued density monitoring of the species is recommended.

6. Brown hyaena ranging behaviour and activity in relation to land use and roads

6.1. Introduction

Predators use their environments strategically to meet their necessary resource requirements and as part of this process they establish home ranges or areas wherein their movements are generally restricted (Powell, 2012). Within home ranges, some areas are used more intensively than others (Powell, 2000). Utilisation distribution (UD) is therefore an important part of movement ecology (Getz and Wilmers, 2004; Keating and Cherry, 2009; Van Winkle, 1975; Worton, 1989). In response to environmental changes or competition, home ranges and UD shift throughout an animal's lifetime (Powell, 2012), thus making studies which examine animals' spatial interactions especially important for conservation management (Simcharoen *et al.*, 2008).

One of the most accurate methods for determining home range size and UD is by affixing global positioning system (GPS) collars to study animals (Cagnacci *et al.*, 2010; Kochanny *et al.*, 2009; Pebsworth *et al.*, 2012). GPS collar data can reveal 24-hour information about a species' use of the environment even when the animal is unobservable (Cagnacci *et al.*, 2010). Studies that used very high frequency (VHF) and GPS collars in extensive and challenging landscapes revealed that GPS collars provide more useful and precise information (Ballard *et al.*, 1998; Kochanny *et al.*, 2009; McCarthy *et al.*, 2005; Ruth *et al.*, 2010).

In recent years, collar data have been used to understand how animals respond to human presence and anthropogenic-induced changes to the landscape (Graham *et al.*, 2009; Valiex *et al.*, 2012). This is especially important to inform conservation management decisions (Cagnacci *et al.*, 2010). However, sample sizes from collar data are often small due to the high costs of collaring, premature death of study animals, or

challenges in relocating collared individuals (Marnewick and Somers, 2015; Powell, 2012; Stratford and Stratford, 2011). Cautious interpretation of data is necessary with small sample sizes (Börger *et al.*, 2006; McCarthy *et al.*, 2005).

This chapter examines data from two collared brown hyaenas; one resident in a montane environment with lower human impacts and the second based on the flatlands below the Soutpansberg Mountains where human activity is more prevalent and varied. Home range estimates and UD are constructed for both individuals. A comparative assessment of brown hyaena activity levels and utilisation in relation to land use types (LUTs) and roads is conducted to determine how brown hyaenas respond to human-dominated environments. Interviews confirm that game farmers are more tolerant towards brown hyaenas and other predators than livestock farmers (Chapter 4). Tourism operators are the most tolerant towards predators (Chapter 3). UD and activity levels are considered in relation to landowners' attitudes.

6.1.1. Factors affecting home range size

Over time animals develop an understanding of their environment that is used to meet daily requirements and avoid danger based upon a constantly evolving cognitive spatial map within their hippocampus (Fyhn *et al.*, 2004; O'Keefe and Dostrovsky, 1971). Ranging behaviour is dictated by information contained within an animal's spatial map (Gautestad, 2011), and this influences home range size and changes in ranging over time (Powell, 2012).

In general, large sized mammals tend to have bigger home ranges, longer day ranges and use home ranges at a higher temporal rate than smaller mammals (Carbone *et al.*, 2005; Harestad and Bunnell, 1979; McNab, 1963; Swihart *et al.*, 1988). Large bodied animals need large home ranges to meet their greater metabolic and biological requirements (Gittleman and Harvey, 1982; McNab, 1963). The resource dispersion hypothesis suggests that home range size in carnivores is affected by resource availability rather than population constraints (Macdonald, 1983). A large predator's home range must encompass an ample prey base, provide sufficient mate selection,

avoid competitors, and meet habitat requirements (Gittleman and Harvey, 1982; Macdonald, 1983; Maputla *et al.*, 2015; Mizutani and Jewell, 1998; Powell, 2012). For example, spotted hyaenas' use of space in the Masai Mara National Reserve, Kenya was dependent upon variables such as den location, distribution of prey, water features, and vegetation types (Kolowski and Holekamp, 2009).

6.1.2. Brown hyaena home ranges

Most brown hyaenas are territorial clan members with only 8% of all subadult and adult brown hyaenas displaying nomadic behaviour (Mills, 1982b; Mills, 1990). Individuals within a clan often have similar and overlapping home ranges and a tendency to travel the same pathways (Owens and Owens, 1978; Skinner *et al.*, 1995). Olfactory messages communicated through anal pastings and latrines contribute towards a collective development of the clan's spatial map (Mills, 1987).

Brown hyaena home ranges vary in size depending on environmental, prey, and seasonal factors (Owens and Owens, 1996). A wide variety of home range estimates have been recorded across southern Africa from extremely small ranges – 42.62 km² for an individual brown hyaena in Kwande Private Game Reserve, South Africa (Welch *et al.*, 2016) and an average home range of 21.1 km² in Rustenberg Nature Reserve, South Africa (Skinner and van Aarde, 1987) – to extremely large ranges – up to 1,250 km² along the Namibian coast (Wiesel, 2006). However, the majority of brown hyaena home range estimates fall between 100 km² and 500 km² (Kent, 2011; Maude, 2005; Mills, 1982b; Mills, 1983; Owens and Owens, 1996; Skinner *et al.*, 1995; Thorn *et al.*, 2009).

Brown hyaena home range size is significantly smaller in unprotected areas compared to protected areas (Maude, 2005; Richmond-Coggan, 2014). In Botswana, individual brown hyaenas in a cattle farming area have a mean home range estimate of 192 km², while a hyaena living in the nearby national park has an average home range of 447 km² (Maude, 2005). Another study which detected very small brown hyaena home range sizes surmised that the hyaenas' use of farmland might be responsible (Skinner

and van Aarde, 1987). Disparities in home range size between protected and unprotected areas may be attributed to risks associated with human-induced persecution, higher levels of biomass outside of protected areas, and a greater likelihood of apex predators in protected areas (Richmond-Coggan, 2014). These findings corroborate with studies focusing on other scavenging species (DeVault *et al.*, 2004; Hidalgo-Mihart *et al.*, 2004).

In and around the Soutpansberg Mountains, interview data indicates that more livestock farming is situated on the flatlands and therefore predator persecution is higher in these areas (Chapter 4). The flatlands with their greater anthropogenic risks are more similar to unprotected areas in studies by Richmond-Coggan (2014) and Maude (2005) than the mountainous regions. The brown hyaena based in the flatlands is predicted to have a smaller home range than the mountain-dwelling hyaena (hypothesis 6.1). Nightly trajectories are anticipated to be shorter in the flatland-based brown hyaena compared to montane-based hyaena (hypothesis 6.2).

6.1.3. Behavioural and ranging responses to human activity

The influence of natural forces is important when considering an animal's ranging behaviour, yet humans' effects may be more powerful and more relevant to the conservation agenda. In human-dominated landscapes, human activity affects ranging behaviour in elk (*Cervus elaphus*) more than natural predators or any other factors (Ciuti *et al.*, 2012). African elephants are more active at night and move more quickly in areas of potential human-induced mortality while the opposite effect is found on ranches where elephants are tolerated (Graham *et al.*, 2009). Thus, humans perpetuate a landscape of fear which supersedes wild predation risk (Ciuti *et al.*, 2012).

The landscape of fear concept, which examines how animals regulate their behaviour and distribution in response to predation risk, has primarily been ascribed to prey species (Arias-Del Razo *et al.*, 2012; Coleman and Hill, 2014; Laundre *et al.*, 2001). Recently, this phenomenon has also been observed in apex predators' responses to

humans (Valiex *et al.*, 2012). Many predators adjust their behaviour, ranging, and diet in response to increased human activity and anthropogenic threats (Marker and Dickman, 2005; Rasmussen and Macdonald, 2012; Stillfried *et al.*, 2015; Valiex *et al.*, 2012). African wild dogs, a diurnal species, hunt at night in areas of high human presence and persecution (Rasmussen and Macdonald, 2012). GPS collared lions in human-dominated environments adjust their temporal overlap to avoid times when humans are most active and move at higher speeds in these areas to reduce the amount of time spent there (Valiex *et al.*, 2012). Leopards in Kaeng Krachen National Park, Thailand, exhibit higher nocturnal activity and alter movement patterns near areas that are heavily populated by people (Ngoprasert *et al.*, 2007).

In most systems, a prey species' landscape of fear must consider predation risks from multiple predators which may be utilising different parts of the ecosystem; for example a prey species may need to remain vigilant against terrestrial and aerial predators simultaneously (Coleman, 2013; Willems and Hill, 2009). When considering the human-induced landscape of fear, predators are equally susceptible to double-edged (or more) threats. For example, successful navigation of an area requires predators to respond to risks of direct human persecution such as hunting, and indirect threats like collisions on roads (Stillfried *et al.*, 2015). It is hypothesised that brown hyaenas will spend less time and exert higher activity levels in LUTs where anthropogenic risk is presumed higher (mainly livestock farms) to minimise exposure to human risks (hypothesis 6.3).

6.1.4. Risks and advantages of road usage

Although carnivores are less likely to be killed on roads than herbivores (Barthelmess and Brooks, 2010), roads still present a very real danger (Grilo *et al.*, 2009; Kerley *et al.*, 2002). Roads attract scavengers because roadkills offer an easy meal (Mohammadi and Kaboli, 2016). Consequently, striped hyaenas are frequently killed through road mortality in Iran (Mohammadi and Kaboli, 2016). Some carnivores have adopted road avoidance techniques in response to traffic hazards such as wolves (Whittington *et al.*, 2005) and wolverines (*Gulo gulo*) (Copeland *et al.*, 2007). Despite the risks, many

animals prefer roads because of their ease of unimpeded travel (Brown *et al.*, 2006; Hines *et al.*, 2010). Brown hyaenas have an affinity with roads because they are used as territorial boundaries and travel corridors (Burgener and Gusset, 2003; Hulsman *et al.*, 2010; Richmond-Coggan, 2014). Proximity to roads is the strongest factor determining brown hyaena use of space within reserves (Welch *et al.*, 2016). Despite greater potential persecution in non-protected areas, which may be associated with higher exposure by using more open road systems, road usage is equally high in protected and non-protected areas (Richmond-Coggan, 2014). It is predicted that, in line with other studies, brown hyaenas will show a preference for roads (hypothesis 6.4).

6.2. Methods

6.2.1. Capturing and collaring brown hyaenas

I used camera trap data collected by the Primate and Predator Project (PPP) at Lajuma Research Centre to identify areas where brown hyaenas frequently move. I set up soft hold foot loops (Figure 6.1a) along game trails in these areas (Figure 6.1b). The foot loop system is more effective and more humane for predators than box trapping (Frank *et al.*, 2003; Goodrich *et al.*, 2001; Logan *et al.*, 1999). Box trapping has received criticism for crushing animals' tails when the heavy metal door comes down and for snapping predator's canines when they bite the metal sidings (Karanth *et al.*, 2010). However, some studies debate that the traditional box trapping approach is less stressful for the animal and causes less injury (Iossa *et al.*, 2007). Ultimately, the most important component of safe and effective trapping is to ensure that the methods employed are well designed, use quality equipment, and that trained practitioners place animal and human welfare at the forefront of the procedure (Proulx *et al.*, 2012).

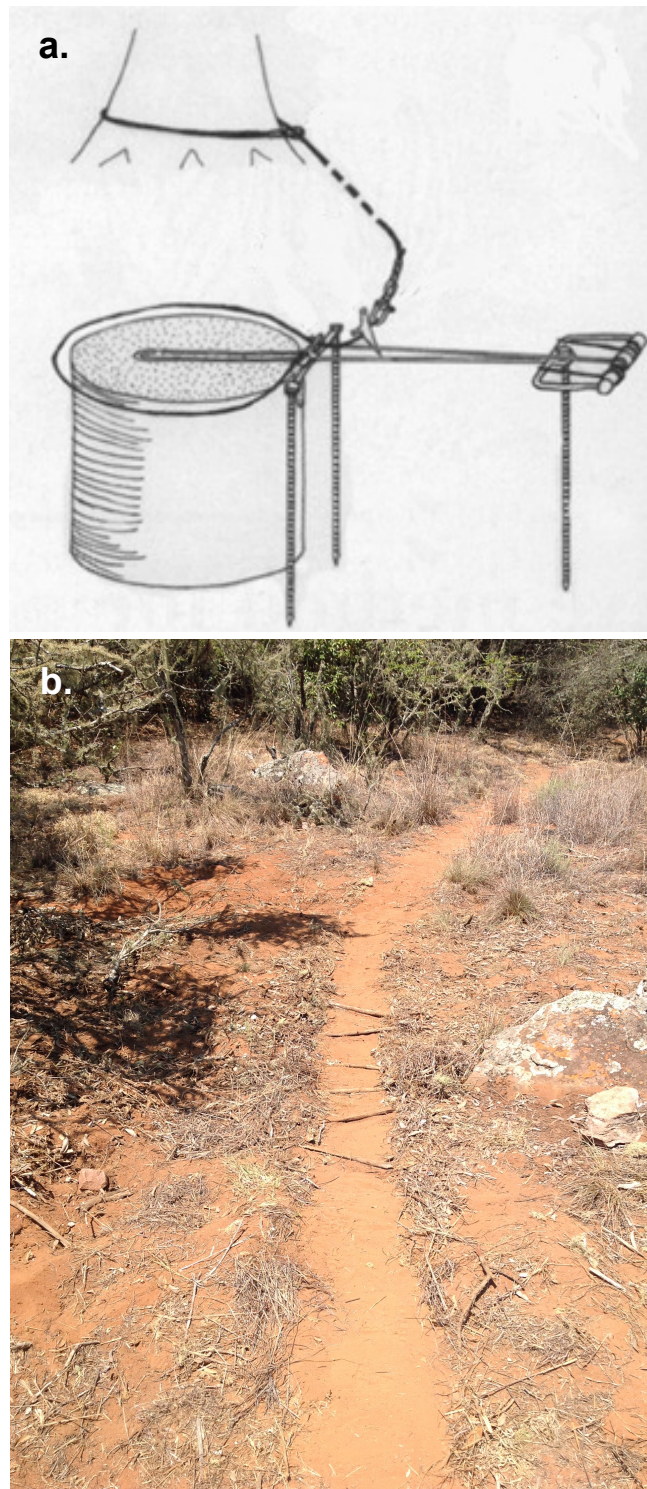


Figure 6.1 a. Soft hold foot loop. Image adapted from Frank *et al.* (2003). b. A completed trap site at Lajuma Research Centre. The foot loop is hidden under fine dirt on a game trail. Sticks are used to guide the hyaena's foot onto the central trigger plate.

No bait was used and the foot loop was completely covered by a light layer of soil, making the trap invisible. The game trail appeared completely natural aside from a few guiding sticks placed around the hidden trigger plate (Figure 6.1b) This 'blind set'

system proved to be more successful for catching brown hyaenas at Lajuma than the baited boma trap system used for leopards.

All brown hyaenas were caught and collared on the Lajuma property. Eight concealed foot loops were opened nightly when a veterinarian was available from 17:00 to 6:00 to coincide with hyaena activity patterns. I checked traps by vehicle at 23:00 and 6:00. Trap site transmitters (VHF Trapsite Transmitters TBT-503-1, Telonics, Mesa, AZ, USA), which emit a VHF radio signal when a trap has been triggered, offered early warning of a capture prior to arriving at the scene. A South African Veterinary Council registered veterinarian administered an appropriate amount of Zoletil based on the animal's estimated weight (standard darts contained just under 200 mg of Zoletil) using an air pressured dart gun (Dan-Inject CO₂ Injection Rifle Model JM.DB.13, Dan-Inject ApS, Børkop, Denmark). Once immobilised, the vet closely monitored the hyaena and treated any skin injuries. I weighed the animal and attached a GPS collar (GPS Plus collar, Vectronic Aerospace GmbH, Berlin, Germany). The foot loop was removed after the vet deemed the animal recumbent.

The collar was fitted to the animals' neck securely with sufficient space for growth and swallowing (Figure 6.2). I tested the collar's ultra high frequency (UHF) and VHF functions during the collaring process to ensure the collar was sending and receiving data. Sometimes this was not possible due to the selective time frame that the collar is actively communicating, but testing was completed regularly during the trapping period to guarantee proper functioning of equipment. While the animal was immobilised, I took body measurements and photographs, and conducted dentition assessments. The veterinarian inserted a microchip for future identification purposes.



Figure 6.2 Taking data and collaring brown hyaena AM1 on March 7, 2013 at Lajuma Research Centre.

Total collar mass is recommended at between or below 3 - 5% of the study animal's body weight to avoid influencing behaviour and reducing survivorship (Macdonald and Amlaner, 1980). There is little evidence of collars negatively affecting predators' hunting success, food intake, or reproductive success if the recommended percentile is adhered to (Laurenson and Caro, 1994). Vectronic GPS Plus collars weigh 1,050 g. The lowest safe weight of a brown hyaena able to carry this collar is 21 kg. The smallest hyaena I captured weighed 33.32 kg and the average weight of brown hyaenas caught during this survey was 36.6 kg. Therefore, the collars weighed 2.87% of the average brown hyaena's body mass, which was well below the recommended weight threshold.

Collaring and all morphological assessments were completed within one hour depending on when the animal showed the first signs of recovery. The hyaena was secured in a wooden recovery crate to prevent injury while waking up (Stratford and Stratford, 2011). When the vet declared that the hyaena had recuperated from the immobilisation drugs, I released the animal.

The GPS collars were programmed to stay on the animals for 455 days and then drop off automatically so that animals do not have to be recaptured a second time to recover equipment and data which is less stressful for the animals and easier for

researchers, especially in difficult environments (Karanth *et al.*, 2010). The collars logged the hyaena's GPS location at hourly intervals between 18:00 and 7:00 daily. UHF data was downloaded on demand using a GPS Plus Handheld Terminal (Vectronic Aerospace GmbH, Berlin, Germany) from about a two-kilometre proximity of the collar depending on topography and was also retrieved from the store on-board function once a detached collar was retrieved. I extracted data directly from the store on board collars or via the UHF terminal using GPS Plus Collar Manager software (Vectronic Aerospace GmbH, Berlin, Germany).

Recovering the data was more problematic than anticipated. Despite numerous attempts and innovative strategies to communicate with the collars using the UHF terminal, I was unable to recover any data for a year after the first animal was collared. The only successful method of relocating the collared hyaenas was flying by helicopter and radio tracking the animals with VHF receivers (R-1000 Telemetry Receiver, Communications Specialists Inc., Orange, CA, USA) connected to antennas affixed to the helicopter's landing skids. The distance of collar communication dramatically increases from the air (Mech *et al.*, 1990). I was able to recover all data from two hyaenas, but even by air I did not relocate two collared individuals following release.

6.2.2. Data analysis

6.2.2.1. Home range and UD analysis

I selected home range and UD metrics based on their alignment with *a priori* hypotheses, research questions, and knowledge of the study environment (Fieberg and Boerger, 2012; Kie *et al.*, 2010; Powell, 2000; Signer *et al.*, 2015).

Time Local Convex Hull (T-LoCoH) was the main method for home range and UD analysis because of its ability to determine UD across seasons within a rugged environment (Lichti and Swihart, 2011; Lyons *et al.*, 2013). Local convex hull (LoCoH) analysis is a non-parametric kernel density estimation that accommodates for high and

low usage within the range by creating convex hulls around data points which ascertains utilisation distribution (Getz *et al.*, 2007; Getz and Wilmers, 2004). LoCoH has recently evolved to incorporate temporal variation under the acronym T-LoCoH (Lyons *et al.*, 2013). The date-time stamp of each location in relation to nearest neighbours is incorporated into the LoCoH algorithm through the inclusion of a time-scaled distance metric (TSD) (Lyons *et al.*, 2013). Through this process, a third axis of Euclidean space is introduced which estimates the greatest distance an individual could have travelled during a specified time period (Lyons *et al.*, 2013).

The adaptive LoCoH method was employed as more defined isopleths are given in areas where data is most abundant, creating more accurate results (Getz *et al.*, 2007). As a caveat of the adaptive method, the maximum distance between two points in the dataset is required. This was measured in QGIS (Quantum GIS Development Team, 2014) and set as the value a (Getz *et al.*, 2007). For hyaena AM1 a was set at 22.3 km and a was set at 24.03 km for hyaena AF3. I determined the TSD using graphical tools in R (Lyons *et al.*, 2013), resulting in a TSD of 0.04 for AM1 and a TSD of 0.035 for AF3.

I calculated minimum area convex polygon (MCP) for backwards comparability with estimates of brown hyaena home ranges elsewhere (Houser *et al.*, 2009; Marnewick and Somers, 2015; Swanepoel, 2008). MCP estimates the area an animal uses by creating a circumference around the outer limits of all recorded points (Hayne, 1949; Mohr, 1947). The plugin Animove estimated MCP in QGIS (González *et al.*, 2014). MCP was secondary to T-LoCoH because there are numerous limitations to MCP including overestimating the range size, assuming that all areas within the range are used evenly, ignoring valuable information pertaining to central and more utilised points, and failing to acknowledge unoccupied areas within the polygon (Getz *et al.*, 2007; Powell, 2000; Worton, 1987).

In line with tradition home range estimation methods, I selected a 95% isopleth (95% of all GPS points) to signify overall range usage (Baker *et al.*, 2015; Powell, 2012). I selected a 50% density quartile (50% of all GPS points) to indicate the most intensely used areas or core areas (Marnewick and Somers, 2015; Richmond-Coggan, 2014).

Due to animals' decisive movements in their environments, autocorrelation or temporally interrelated points within a dataset can occur (Rooney *et al.*, 1998). Traditionally, methods have been employed to correct for this but more recently autocorrelation has been labeled a 'red herring' which diverts attention from gathering representative sample sizes (Fieberg, 2007) or increases error within the data after subsampling (Rooney *et al.*, 1998). I did not apply autocorrelation corrections due to the regularity of sampling between data points, the large distances moved by brown hyaenas nightly, and a desire to protect the data's biological integrity (de Solla *et al.*, 1999; Rooney *et al.*, 1998).

I graphed home ranges (95% T-LoCoH) as cumulative observation-area curves for both hyaenas to check whether home range estimates reached asymptote. It is recommended that only data sets where asymptote is reached are included in home ranges to avoid 'dubious comparisons' (Laver and Kelly, 2008, p. 294).

6.2.2.2. Activity time budgets

Dual-axis gravitational accelerometers within the GPS collars collected activity data four times per second and recorded average activity levels at two-minute intervals. Acceleration was measured in forward and backward motions (X axis) and sideways and rotary motions (Y axis) (Krop-Benesch *et al.*, 2011). Activity levels ranged between 0 (no activity) and 255 (high activity) (Krop-Benesch *et al.*, 2011). There is a strong correlation between X axis and Y axis activity data (Löttker *et al.*, 2009; Podolski *et al.*, 2013; Stache *et al.*, 2013), therefore, in line with other studies, I only analysed X axis data (Angel, 2015; Heurich *et al.*, 2014; Podolski *et al.*, 2013). I used Activity Pattern version 1.3.1 and Activity Explorer (Vectronic Aerospace GmbH, Berlin, Germany) to analyse activity patterns.

I tested the level of activity during daytime hours using a Wilcoxon rank sum test to determine if there was a statistical difference between the two hyaenas. The level of nighttime activity was also analysed in a similar fashion. Day was defined as 06:00 to 17:59. Night was demarcated as 18:00 to 05:59.

6.2.2.3. Nightly trajectories

I measured GPS points taken from dusk till dawn chronologically in QGIS (Quantum GIS Development Team, 2014) to determine nightly trajectory distances. Distances may be skewed because a straight line is measured between GPS points while the animal may have wandered (Powell, 2012). However, a close proximity between data points, as was used in this study, is the best way to counter these inconsistencies (Powell, 2012). The distances of nightly trajectories were tested for significance between the two study animals using a Wilcoxon rank sum test.

6.2.2.4. Land use types

I categorised all properties within the brown hyaenas' 95% and 50% T-LoCoH home ranges by land use type based on personal knowledge of the area, communication with local landowners, and interview data.

The following LUT categories were used:

- *Agriculture*: land used for growing and selling fruit or vegetable products, also includes commercial mining of salt from saltpans
- *Game farming*: land used for breeding and selling game, often partaking in commercial hunting of game species
- *Livestock farming*: land used for breeding and selling livestock, sales are either as a live commodity or as meat
- *Tourism*: land used for tourism or personal leisure, this also includes properties devoted to research purposes

Although some landowners engaged in multiple land uses (refer to Table 3.1 as an example), for simplicity of categorisation only the predominate LUT was assigned. I measured the area of each LUT within each hyaena's 95% home range and 50% core area in QGIS (Quantum GIS Development Team, 2014) to determine the proportion of the home range each LUT comprised. I counted the number of GPS points in each LUT for both hyaenas. G-Tests ascertained whether the number of observed GPS points per

LUT was significantly different from the expected number of points, taking into consideration the proportion of the total area that each LUT encompassed.

6.2.2.5. Road usage

I used a government issued map of roads and personal mapping of the area to chart and categorise roads based on their substrate (tarmac or dirt). Following Richmond-Coggan (2014), I created a 50 m buffer around all roads within the hyaenas' 95% T-LoCoH home ranges to accommodate for GPS points which are displaced slightly by positional errors in GPS accuracy (Moen *et al.*, 1997). I calculated the number of GPS points that fell entirely within the 50 m road buffers for each brown hyaena. I gauged the total area of tarmac and dirt road buffer zones within a brown hyaena's home range (95% T-LoCoH) and core area (50% T-LoCoH). This was subtracted from the entire home range area to determine the area of non-road land. G-Tests tested observed and expected road usage to determine whether road or non-road areas are preferred, and whether road substrate has an effect.

6.2.2.6. Activity levels in relation to LUTs

Activity data points were spatially aligned with GPS data points in QGIS (Quantum GIS Development Team, 2014) to construct datasets of activity data within LUTs. Although the accelerometers collected data 24 hours a day, GPS point collection only occurred at night, therefore analysis of activity levels in relation to LUTs was confined to nocturnal periods. Kruskal Wallis tests assessed whether hyaenas modify their activity levels in different LUTs in 95% T-LoCoH home ranges and 50% T-LoCoH core areas. Post-hoc tests and graphing of means determined differences between LUTs and the effects of results.

6.3. Results

I fitted GPS collars to four adult brown hyaenas (Table 6.1). Data was only recovered from two individuals (AM1 and AF3).

Table 6.1 Brown hyaenas fitted with GPS collars at Lajuma Research Centre in 2013.

Name	Sex	Weight (kg)	Date collared	Collar release date	Data points recorded	Successful fix rate
Adult female 1 (AF1)	Female	37.37	26/02/13	27/05/14	N/A	N/A
Adult male 1 (AM1)	Male	39.32	07/03/13	05/06/14	6,232	98%
Adult female 2 (AF2)	Female	36.37	15/09/13	14/12/14	N/A	N/A
Adult female 3 (AF3)	Female	33.32	15/10/13	13/01/15	2,332	85.30%

AM1 wore a collar for the entire duration of the collar's 455-day lifespan and a full set of data points was recovered during this period. Humans killed AF3 197 days after collaring. AF3's collar was removed from the animal postmortem and disposed of at an alternate location. Despite attempts made by whoever killed AF3 to destroy the collar, the collar's VHF signal remained functional and the collar was recovered. AF3's body was not located and the cause of AF3's death is unknown.

AM1 was resident in a largely montane area throughout the data collection period. Post-collaring, AF3 travelled northwest until she reached low-lying areas and resided off the mountains, yet near the base, until her death. Aside from 32 data points taken during AF3's exit from the mountains in the two days immediately following AF3's collaring, there is no home range overlap between AM1 and AF3 (Figure 6.3).

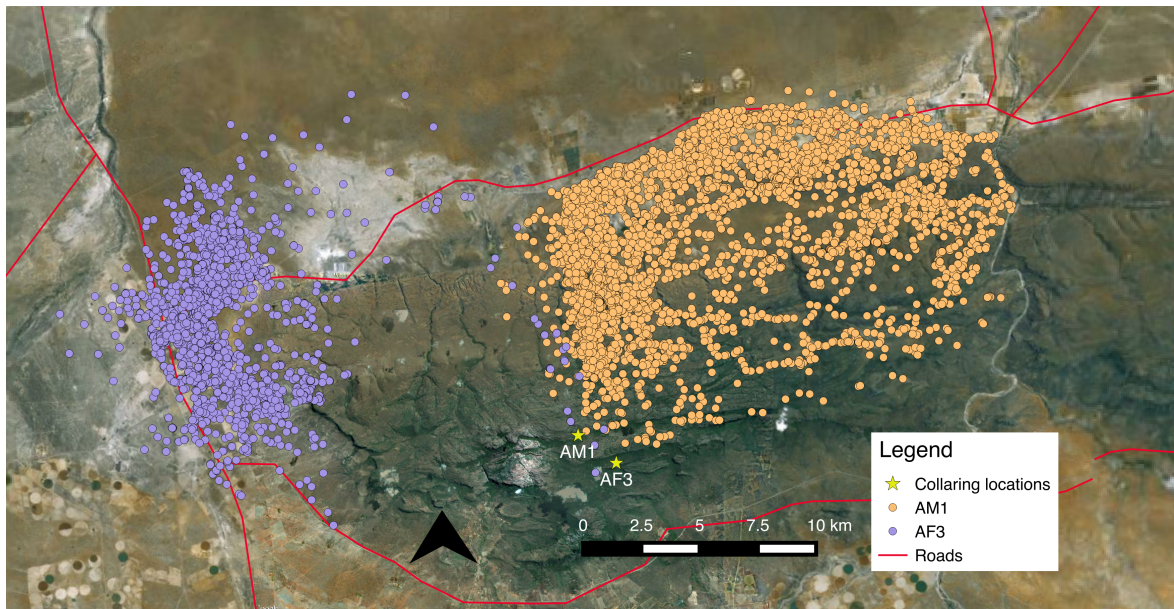


Figure 6.3 GPS locations and collaring locations of collared brown hyaenas AM1 and AF3 in and around the Soutpansberg Mountains. Roads indicate tarmac roads.

6.3.1. Home ranges and utilisation distribution

Home range estimates (95% T-LoCoH) reach asymptote in both hyaenas (Figure 6.4).

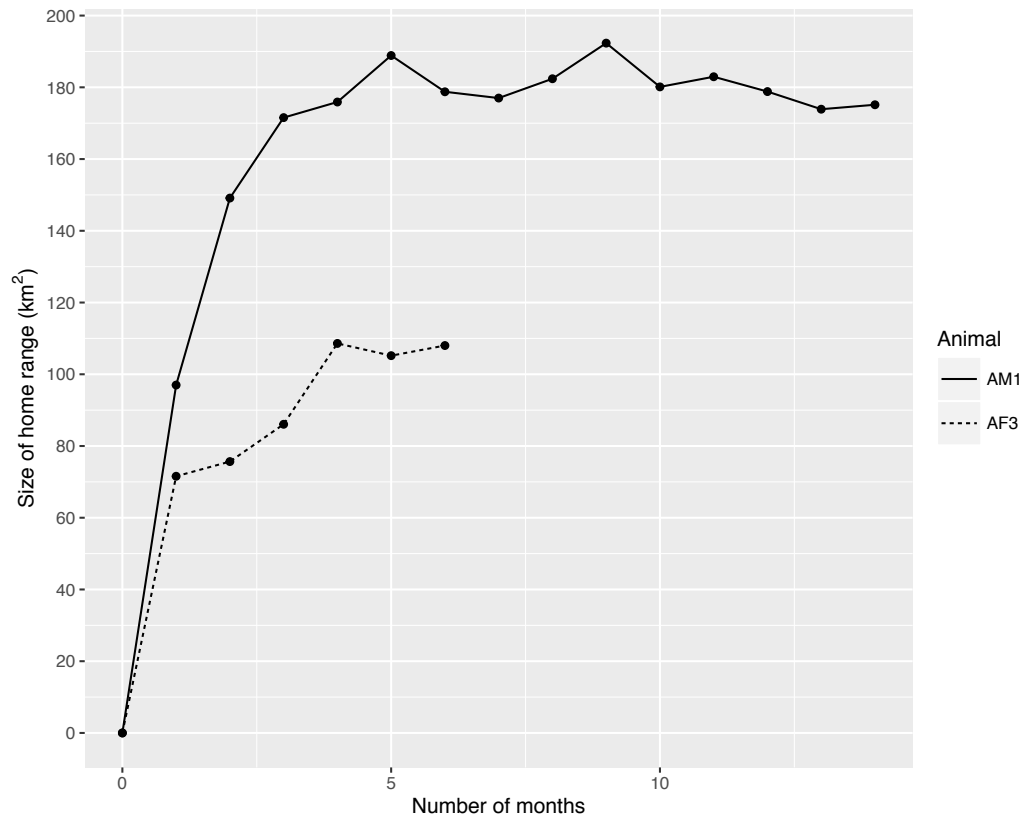


Figure 6.4 Brown hyaena home range sizes (95% T-LoCoH) in and around the Soutpansberg Mountains plotted against the number of data collection months. Asymptote is reached after four months in both hyaenas.

T-LoCoH and MCP estimators indicate that AF3 has a smaller home range and core area than AM1 (Table 6.2). T-LoCoH estimates are smaller than MCP estimates.

Table 6.2 Estimates of brown hyaena 95% home ranges and 50% core areas using MCP and T-LoCoH estimators in and around the Soutpansberg Mountains.

Name	Data points	Sampling days	MCP core area 50% (km ²)	MCP home range 95% (km ²)	T-LoCoH core area 50% (km ²)	T-LoCoH home range 95% (km ²)
AM1	6,322	455	94.01	221.13	68.52	169.79
AF3	2,332	197	27.21	103.02	26.32	95.04

Both brown hyaenas have almost identically sized areas that they use the most frequently (10% and 25% isopleths) (Figure 6.5). Isopleth usage at 0.1 (10%) is 15.16 km² in AM1 and 14.45 km² in AF3. At 0.25 isopleth usage (25%), AM1 uses 19.79 km² and AF3 uses 20.16 km².

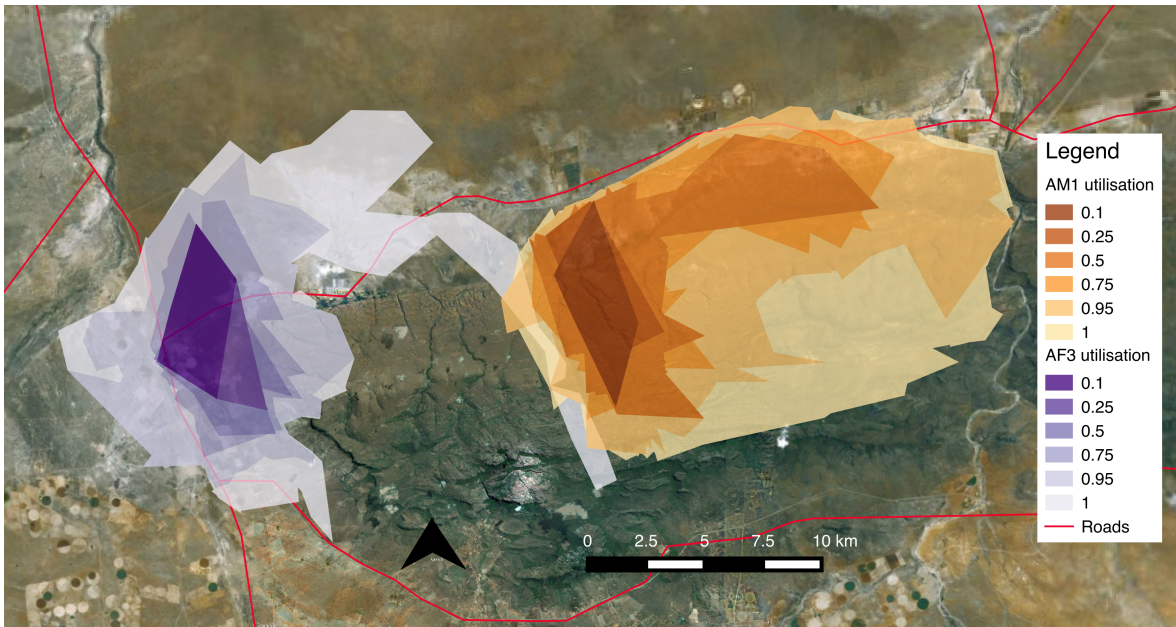


Figure 6.5 T-LoCoH utilisation distribution for collared brown hyaenas AM1 and AF3 in and around the Soutpansberg Mountains. Darker colours indicate higher usage in relation to percentage isopleths, ranging from high (0.1 (10%)) to low (1 (100%)). Roads indicate tarmac roads.

6.3.2. Activity time budgets

Both hyaenas are primarily nocturnal (Figure 6.6). There is a significant difference in average hourly activity levels during the day between AM1 and AF3 (Wilcoxon rank sum: $W = 28$, $p = 0.01$). AF3 is slightly more active during daylight hours than AM1, although daytime activity is extremely rare in both individuals. There is also a significant difference in average hourly activity levels during the night between the two hyaenas (Wilcoxon rank sum: $W = 111$, $p = 0.0242$). During hours of peak activity, AF3 has a lower mean activity level indicating that movement is slower overall.

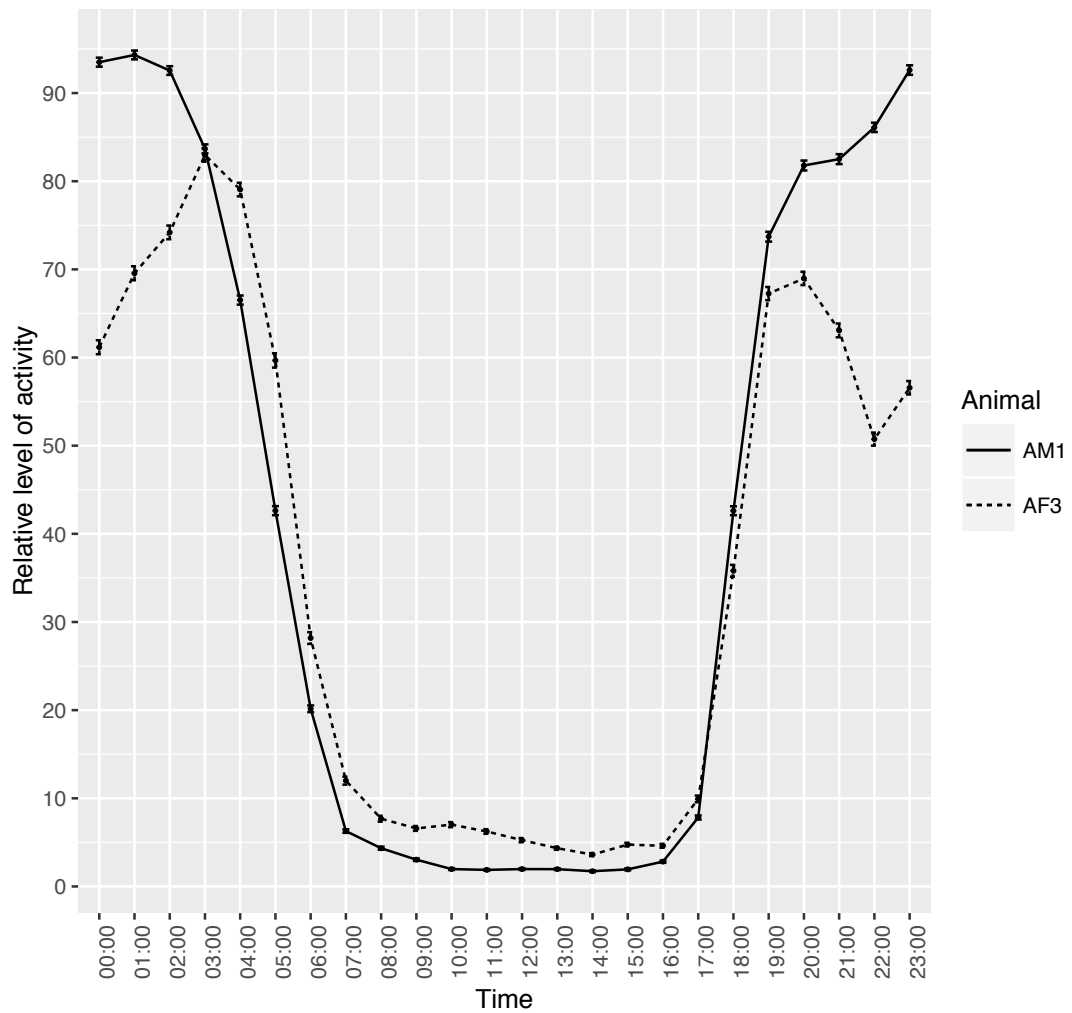


Figure 6.6 Mean brown hyaena activity by time in and around the Soutpansberg Mountains. Bars indicate standard error.

6.3.3. Nightly trajectories

A significant difference was detected between distances in nightly trajectories for AM1 and AF3 (Wilcoxon rank sum: $W = 70431$, $p < 2.2e-16$). AM1's shortest nightly distance is 0.47 km and the longest is 37.72 km with an average nightly trajectory of 17.02 km. AF3 generally moves shorter nightly distances. Her nightly path lengths vary between 0.13 km and 24.73 km with an average distance of 9.72 km.

6.3.4. Land use type utilisation

The study animals confine their movements to privately owned land. Game farming comprises the biggest proportion of the 95% and 50% T-LoCoH home ranges for both brown hyaenas (Figure 6.7). Within AM1's home range, properties used for tourism comprise the second largest LUT, although tourism properties account for a smaller proportion of AM1's core area (18.25%) than the 95% home range (38.95%). No tourism properties are present in AF3's range. Properties specialising in livestock farming compose a greater proportion of AF3's whole home range (16.39%) than the core area (6.73%) while the opposite is true with AM1.

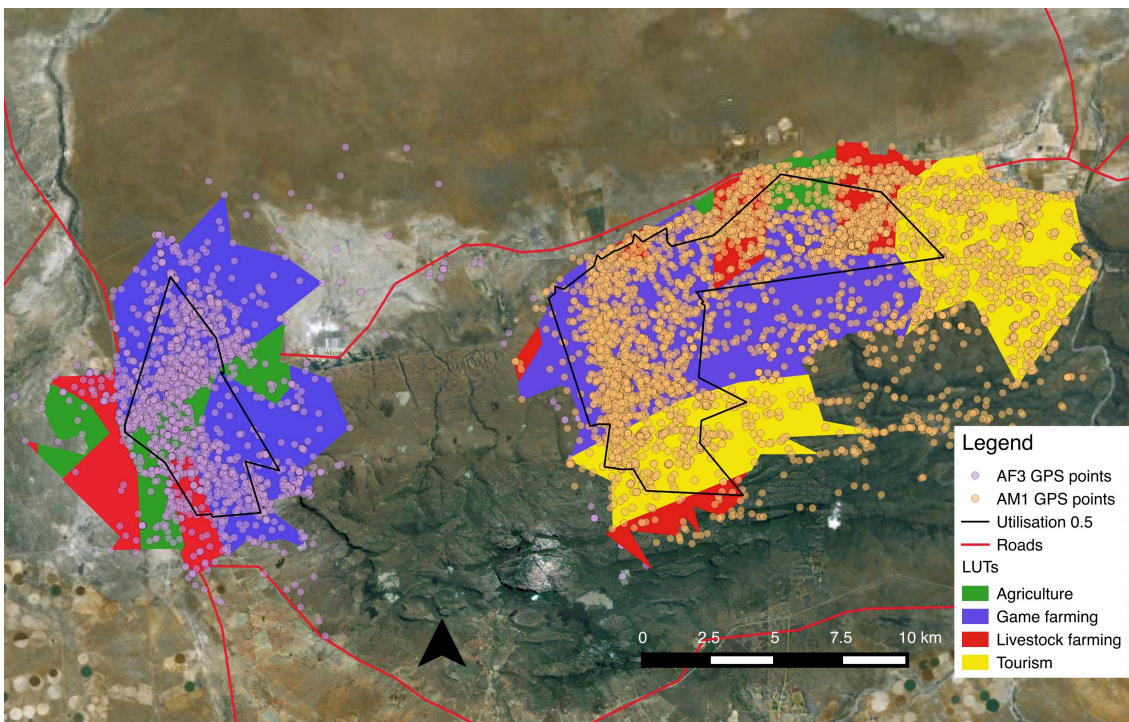


Figure 6.7 Brown hyaena home ranges within the 95% T-LoCoH home range and the 50% T-LoCoH core area in and around the Soutpansberg Mountains in relation to land use types. Adjoining multi-coloured polygons indicate the 95% T-LoCoH home range for AM1 and AF3. Land use variation within these ranges is indicated by colour. Black lines represent 50% T-LoCoH core areas for AM1 and AF3. Roads indicate tarmac roads.

Brown hyaenas use LUTs preferentially rather than in relation to availability in their 95% T-LoCoH home ranges (G -Test: $G = 605.01$, $df = 3$, $p < 2.2e-16$) and their 50% T-LoCoH core areas (G -Test: $G = 1512.5$, $df = 3$, $p < 2.2e-16$). Hyaenas use game farming areas significantly more than expected and tourism areas significantly less than

expected (Figure 6.8). Variation between the observed and expected use of livestock and agricultural areas are less pronounced, but livestock farm usage is higher than expected while time spent on agricultural farms is lower.

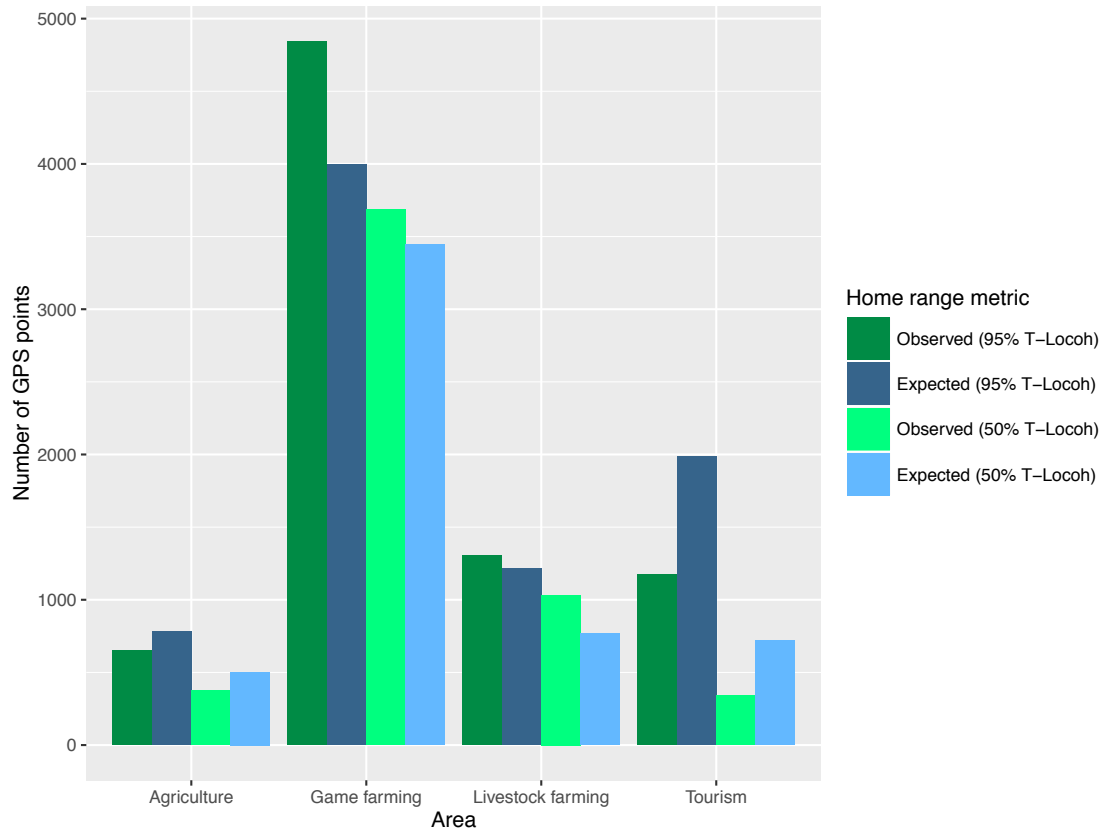


Figure 6.8 Number of observed and expected GPS points for brown hyaenas in each land use type within the 95% T-LoCoH home range and the 50% T-LoCoH core area in and around the Soutpansberg Mountains.

6.3.5. Road usage

AM1's territory is bounded by clear geographic features on two sides (Figure 6.3). On the north side is the R523, a 120 km/hr tarmac road which large freighter trucks frequently use to transport goods to and from Zimbabwe 24 hours a day. On the east side is the Sand River gorge. The southern and western borders lack apparent geographical features. AM1 crosses the tarmac road relatively infrequently (29 out of 455 nights) (Table 6.3). The majority of these crossings are paired (89.65%), meaning that AM1 crosses the road and then returns later the same night. During non-paired occasions ($n = 3$), AM1 crosses the tarmac road four times in a night.

No apparent geographical features bound AF3's home range. Three fast-moving tar roads, the R521, the R522 and the R523, bisect the centre of AF3's territory (Figure 6.3). AF3 crosses a fast-moving tarmac road on 120 out of 197 nights (Table 6.3). The frequency of nightly tarmac road crossings is substantially higher than AM1 with up to seven crossings a night recorded.

Table 6.3 Nightly tarmac road crossings of brown hyaenas in and around the Soutpansberg Mountains.

Number of road crossings a night	Total nights	
	AM1	AF3
1	1	30
2	25	40
3	0	23
4	3	17
5	0	5
6	0	3
7	0	2
Total crossings	29	120
Percentage of all nights	6.42	60.91

Brown hyaenas show a significant preference for road usage compared to non-road usage within the 95% T-LoCoH home ranges (G -Test: $G = 238.44$, $df = 1$, $p < 2.2e-16$) and the 50% T-LoCoH core areas (G -Test: $G = 110.8$, $df = 1$, $p < 2.2e-16$) (Figure 6.9).

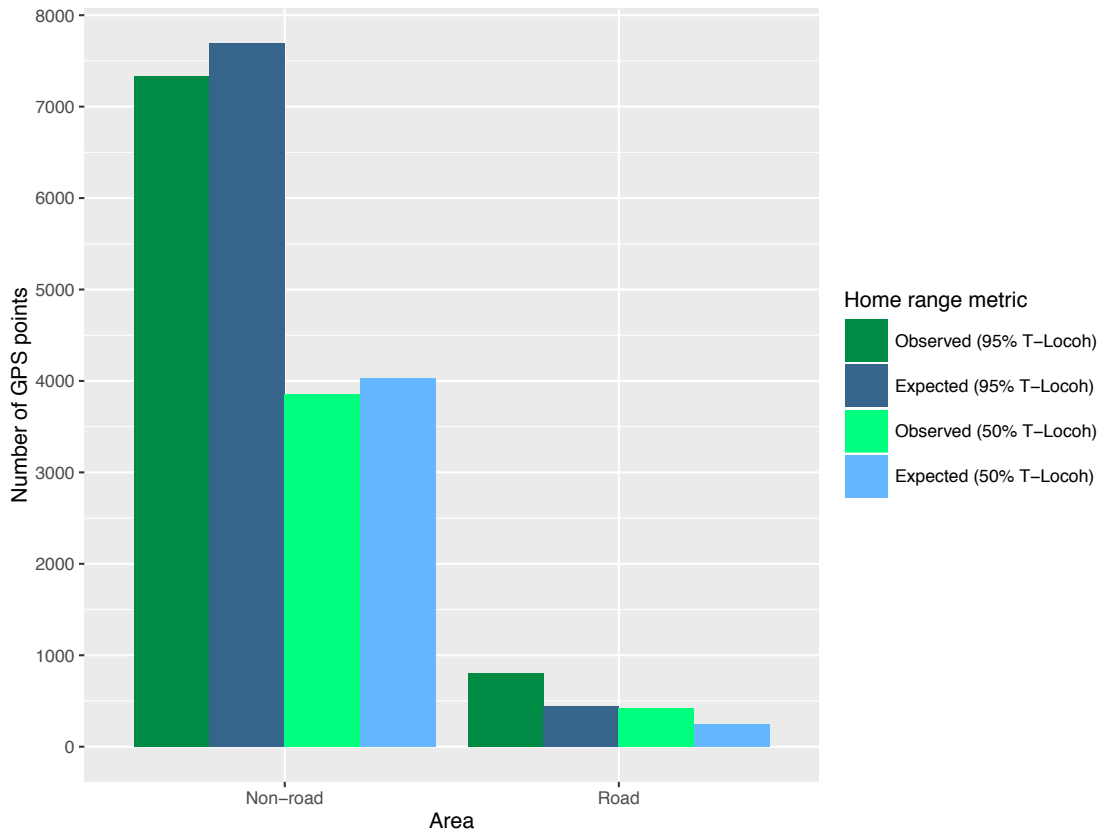


Figure 6.9 Number of observed and expected GPS points for brown hyaenas in road and non-road areas within the 95% T-LoCoH home range and the 50% T-LoCoH core area in and around the Soutpansberg Mountains.

Hyaenas use both tarmac and dirt roads significantly more than expected based on the proportion of their 95% T-LoCoH home ranges (G -Test: $G = 247.31$, $df = 2$, $p < 2.2e-16$) and 50% T-LoCoH core areas (G -Test: $G = 111.19$, $df = 2$, $p < 2.2e-16$) they cover, indicating that substrate does not affect the propensity for usage (Figure 6.10).

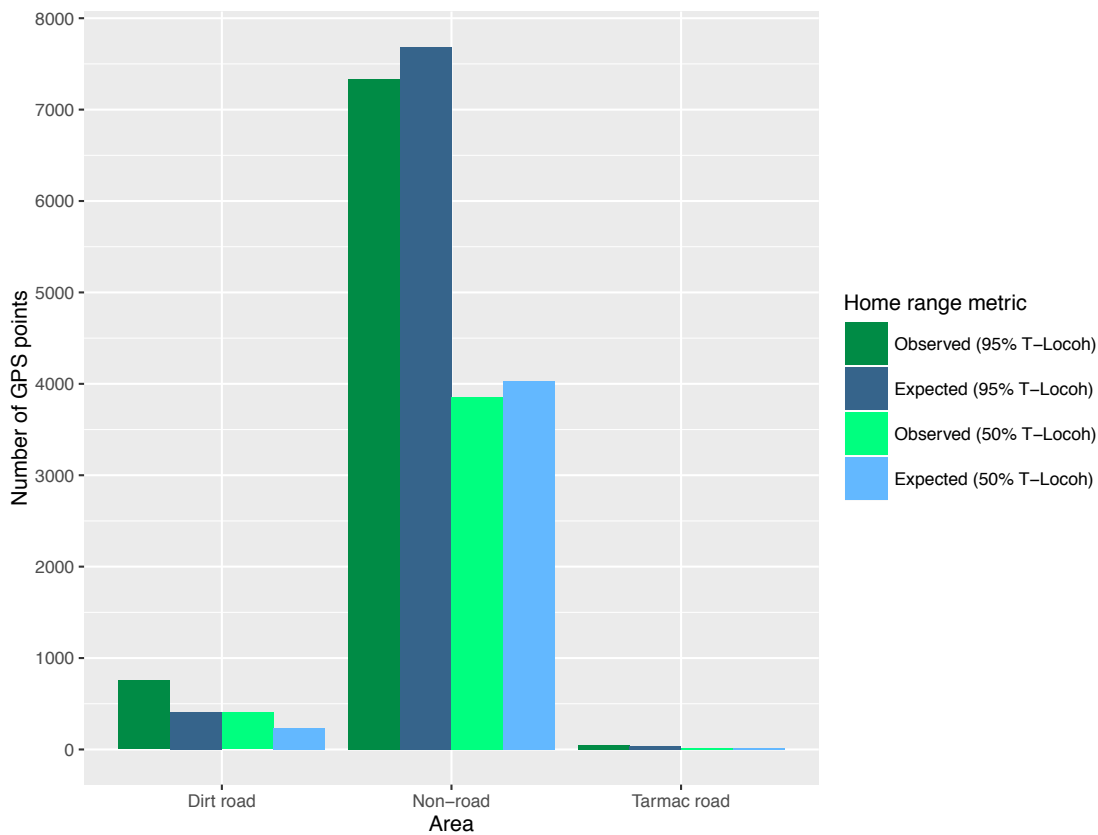


Figure 6.10 Number of observed and expected GPS points for brown hyaenas on tarmac roads, dirt roads, and non-road areas within the 95% T-LoCoH home range and the 50% T-LoCoH core area in and around the Soutpansberg Mountains.

6.3.6. Activity levels in relation to LUTs

A Kruskal Wallis test reveals a significant effect of LUTs on nocturnal activity levels for hyaenas in their 95% T-LoCoH home ranges (Kruskal Wallis: chi squared = 61.248, df = 3, $p = 3.181e-13$). A post-hoc multiple comparison test shows significant differences in the following activity level/LUT relationships: average activity levels are significantly greater in agriculture than game farming areas (observed difference = 243.33, critical difference = 161.34), average activity levels are significantly lower in game farming than livestock farming areas (observed difference = 207.82, critical difference = 143.77), average activity levels are significantly lower in game farming than tourism areas (observed difference = 411.31, critical difference = 159.10), and average activity levels are significantly lower in livestock farming than tourism areas (observed difference = 203.49, critical difference = 195.11) (Figure 6.11).

A similar effect was found for hyaenas in the 50% T-LoCoH core area (Kruskal Wallis: chi squared = 47.205, df = 3, $p = 3.143e-10$). A post-hoc multiple comparison test shows significant differences in activity levels between only two LUT relationships: average activity levels are significantly greater in agriculture than livestock farming areas (observed difference = 166.79, critical difference = 139.49), and are also significantly greater in game farming than livestock farming areas (observed difference = 224.60, critical difference = 88.55) (Figure 6.11).

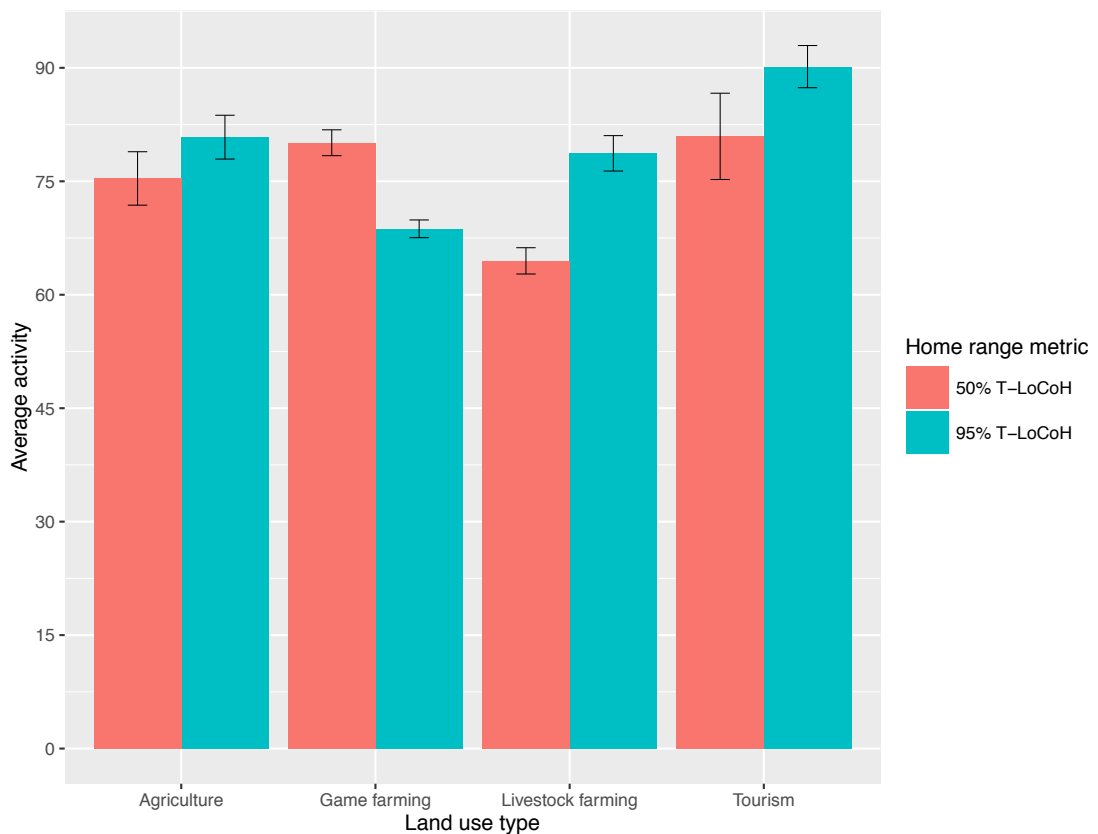


Figure 6.11 Brown hyaena nocturnal activity levels in each LUT within the 95% T-LoCoH home range and the 50% T-LoCoH core area in and around the Soutpansberg Mountains. Bars represent standard error.

6.4. Discussion

Despite considerable effort, I only located two collared brown hyaenas again after release and of these, one collar ceased data collection prematurely. Stratford and Stratford (2011) examined data from two collared spotted hyaenas and acknowledged that their small sample may not represent the wider population. A similar understanding is applied to the interpretation of these data.

The fates of AF1 and AF2 are undetermined. They may have been nomadic individuals, they may have been killed, or they may have experienced collar failure. Although in brown hyaenas nomadism is more common in males, nomadism does occur in females (Mills, 1982b; Owens and Owens, 1996). Collar failure is unlikely, as AF1 and AF2 were never photographed on any camera traps within three multi-scale grids monitored. If a collar malfunctioned but the animal remained local, it probably would be photographed at least once. Based on AF3's human-induced death, occurrences of snaring and other threats to hyaenas discussed in Chapters 3 and 4, and the extreme anthropogenic-induced mortality rate of leopards (Williams *et al.*, in review-b), it is surmised that death, probably as a result of human activity, is the most likely explanation for the disappearance of AF1 and AF2. If the animals died in an enclosed space with no satellite signal such as within a den site, or the collars were destroyed or disposed of sufficiently far away by humans, the collars would become untraceable.

The cause of AF3's death is unknown, but humans almost indisputably caused it. The attempted destruction and hiding of the collar fits with the typical 'shoot, shovel, and shut up' behaviour described by interviewees (Chapter 3). The theory that mountains can act as wildlife refuges (Chase Grey *et al.*, 2013; Gavashelishvili and Lukarevskiy, 2008) might attribute to AM1's survival and AF3's untimely death. Anthropogenic mortality is not uncommon in predators collared for research in southern Africa (Houser *et al.*, 2009; Marnewick and Somers, 2015; Richmond-Coggan, 2014; Skinner and van Aarde, 1987; Williams *et al.*, in review-b). Despite the heavy impact these losses can have on the success of research, recently deaths of study animals have been attracting global media attention around conservation issues such as the death of Cecil the lion in Zimbabwe and wolves 832F and 754 near Yellowstone National Park, USA (Lindsey *et al.*, 2016; Schweber, 2012).

AM1 and AF3 occupy private land. In confirmation of hypothesis 6.3, both hyaenas spend the majority of time in game farming areas, showing a preference for these areas over other LUTs. Leopards in the Waterberg region, South Africa also prefer game farms with some livestock to ecotourism areas or areas used solely for livestock or game farming (Swanepoel, 2008). In Zimbabwe, predator density is significantly

higher on game farms compared to resettled and communal areas (Williams *et al.*, 2016). This may be because human threats are lower on game farming properties compared to other LUTs. Despite tolerance for brown hyaenas on properties used for tourism, hyaenas avoid these areas, suggesting that other factors may be contributing towards LUT preferentiality such as food availability. Game farms may offer greater feeding opportunities than other LUTs. These areas are often stocked with plentiful game and host large predators such as leopards (Swanepoel, 2008) which creates scavenging opportunities (Chapter 7). During hunting season, discarded carcasses and wounded animals on game farms may present additional scavenging opportunities.

In line with other studies (Richmond-Coggan, 2014; Welch *et al.*, 2016) and in acceptance of hypothesis 6.4, brown hyaenas show a preference towards roads. Roads may offer a quicker and unimpeded way for brown hyaenas to move through their territories or present increased scavenging opportunities (Brown *et al.*, 2006; Hines *et al.*, 2010; Mohammadi and Kaboli, 2016). No preferential difference in usage was found between road substrates. A number of species including impalas (Mulero-Pázmány *et al.*, 2015) and black bears (*Ursus americanus*) (Stillfried *et al.*, 2015) show a preference between paved and unpaved roads, and these results are often attributed to avoidance of human threats or high human activity. The lack of differentiation between dirt and tarmac road usage in brown hyaenas may be attributed to their needs as a scavenger to reach a food source before a competing individual, therefore selecting the fastest means possible regardless of risks. AF3 crosses fast-moving tarmac roads regularly due to their unavoidable presence in her home range.

Although vehicle collision is a threat on paved roads, other threats such as areas of high-targeted persecution may be perceived as riskier within a predator's range, as was the case with black bears. Black bears shift their ranges to utilise paved roads away from hunting grounds frequently during hunting season (Stillfried *et al.*, 2015). The frequency of tarmac road crossings and hyaenas' preference for roads suggest that road mortality is a real risk for brown hyaenas in this area. This corresponds with the high level of brown hyaenas killed on roads witnessed by interviewees (Chapter 3).

However, hyaenas may perceive the risks of paved road usage to be lower than spending additional time in risky LUTs hence their continued and preferential usage.

The mountain-dwelling brown hyaena (AM1) has longer nightly trajectories, higher nocturnal activity levels, and a larger home range and core area than the lowland-dwelling hyaena (AF3). These findings accept hypotheses 6.1 and 6.2. This may be because the search for food is harder in the mountainous terrain with less anthropogenic sources and therefore requires more consistent activity and movements over greater distances to meet dietary needs. Brown hyaena nightly ranging distances are often large; yet shorten during periods of food richness (Maude, 2005; Mills, 1990; Skinner and van Aarde, 1987; Skinner *et al.*, 1995). In the Kgalagadi Transfrontier Park where food is intermittent due to desert conditions, brown hyaenas move a mean daily distance of 31.1 km (Mills, 2015). This is longer than the average distance of either hyaena in this study, but it is closer to AM1's average nightly trajectory than AF3's.

Brown hyaenas in unprotected areas have smaller home ranges (Maude, 2005; Richmond-Coggan, 2014). Although both brown hyaenas in this study are resident within unprotected areas, proximity to people is higher on the flatlands where the brown hyaena AF3's home range is smaller. An opposing finding was found in cheetahs whereby human disturbance may cause cheetahs to move further and occupy larger home ranges to avoid conflict (Houser *et al.*, 2009; Marker *et al.*, 2008). This differentiation may be attributed to hyaenas' nocturnal activity patterns compared to cheetahs' diurnal patterns, and to brown hyaenas' scavenging behavior.

Due to the myriad of different methods used to compute home ranges and criticism associated with less robust approaches, comparing modern home range estimates with previous literature may be inaccurate (Laver and Kelly, 2008). However, the home range sizes found in this study were similar to the majority of previous studies (Kent, 2011; Maude, 2005; Mills, 1982b; Mills, 1983; Owens and Owens, 1996; Skinner *et al.*, 1995; Thorn *et al.*, 2009), especially when the more traditionally used 95% MCP values are considered instead of the T-LoCoH values.

An animal's home range can be ambiguous as it is constantly shifting, has diffuse edges, and areas are used with different levels of intensity over time (Powell, 2012). Thus, the boundaries delineated in biological research would be considered insignificant by the animals themselves (Powell, 2012). This fluidity contradicts sharply with the heavily fenced landscape of divided land use types in Limpopo Province. As shown in Chapter 4, there are areas where brown hyaenas are welcome and areas where they are considered less desirable. Analogous with collared cheetahs on unprotected land in Limpopo Province (Marnewick and Somers, 2015), home range size is much larger than ranch size which results in visitations to multiple LUTs and properties. Brown hyaenas move from land where they are considered a bother to land where they are appreciated on a regular basis.

Hyaenas' awareness of threats in each LUT can be surmised from activity level adjustments within different LUTs and preferential use of LUTs. Higher activity levels indicate actions requiring greater acceleration such as running, trotting, attacking, or dragging prey (Nygren, 2015). In certain LUTs, brown hyaenas display higher activity levels, supporting hypothesis 6.3. In line with the theory of predator 'landscape of fear' (Valiex *et al.*, 2012), higher activity levels may be a response to greater human threats and may indicate a deliberate attempt to spend less time in risky areas. Lower average activity on game farms may be attributed to a feeling of security there. The most heavily used den sites within AM1 and AF3's home ranges are within game farming areas. Dens are more likely to be established in these areas due to a greater sense of security. Lower activity levels are associated with denning behaviour. More feeding opportunities may be available on game farms and therefore slower movements during feeding periods would also occur in this LUT. High activity levels on agricultural land where resources are lower may indicate that hyaenas are passing through these areas rather than stopping to feed or den.

AF3's rapid and permanent exodus from the mountains following her collaring might be indicative of a response to perceived human threat. Many animals respond to initial handling through spatial displacement from the capture site, although this displacement is not normally permanent (Moa *et al.*, 2001; Morellet *et al.*, 2009; Ramsay and Stirling, 1986).

The differences found in activity levels between LUTs in the 95% T-LoCoH home ranges and 50% T-LoCoH core areas represent the distinct purposes of core areas and home ranges. The intensely used core area is where less active activities such as sleeping and social interactions often occur while the wider home range also includes long distance foraging and territorial patrolling (Mills, 1990). Due to bias in activity data collected around den sites, activity levels within the 95% T-LoCoH home range present a more valid picture of spatial activity adjustments in brown hyaenas than findings within core areas.

It is convenient for comparative purposes that one collared brown hyaena spends significantly more time in the mountains and the other hyaena stays in the low-lying areas. It is important to reiterate that due to the small sample size, results may elude to trends about utilisation distribution in montane and low-lying areas yet studies with larger sample sizes are more robust so results are more likely to be reflective of population trends. The effect of altitude on brown hyaenas is understudied. Elevational preference is not detected in brown hyaenas in North West Province, South Africa (Thorn *et al.*, 2009), nor in this thesis' occupancy study (Chapter 5). Brown hyaena presence is significantly higher on steeper slopes with higher elevation in Kwandwe Private Game Reserve while the opposite trend is found in Shamwari Private Game Reserve (Welch *et al.*, 2016). This research was conducted in protected areas in South Africa where the importance of mountains as refuges from people may be less prominent. In Namibia, most brown hyaena den sites are hidden in mountainous areas away from the food rich beaches where hyaenas spend a large proportion of their time (Wiesel, 2006). Mountains in this system are considered important for brown hyaenas as a safe area away from competitors and other threats (Wiesel, 2006). The interview data confirms that the Soutpansberg Mountains are viewed as a space separate from people, a place where animals belong (Chapter 4). Many people living in black communities are scared of the mountains or find the terrain inaccessible, therefore reducing the amount of time spent there. Snaring is reported to be more problematic on lower-lying properties. People killed AF3, a lowland-dwelling brown hyaena, indicating that mountains may offer some refuge from anthropogenic threats. Further research is recommended in these two comparative areas with more collared

individuals and the employment of satellite collars to ensure data is recovered regardless of how far hyaenas move in difficult terrains.

Woodroffe and Ginsberg (1998) determined that within any given reserve regardless of its size, large-ranging carnivores are more likely to become extinct than those with smaller ranges, irrespective of their population density. The large home range size of brown hyaenas on and off the mountains increases their vulnerability and indicates the importance of implementing conservation measures in non-protected land for the survival of the species.

6.5. Summary

Unfortunately, data was only recovered from two of four collared brown hyaenas. People killed one of the two traced individuals before data collection was completed. The small sample size renders data valid on an area specific scale but less persuasive for wider population assumptions.

Brown hyaenas in and around the Soutpansberg Mountains have large home ranges, which are comparable in size to those recorded in other parts of southern Africa. The home range of a hyaena, which is predominantly mountain-dwelling, is 169.79 km² (95% T-LoCoH) while a lowland-based hyaena has a smaller home range of 95.04 km² (95% T-LoCoH). The differences in home range size match studies which found that brown hyaenas in protected areas have larger home ranges than those residing in unprotected spaces (Maude, 2005; Richmond-Coggan, 2014). Although neither hyaena occupies an officially protected area, the hyaena residing in the mountains experiences lower anthropogenic risks and therefore more 'protection' than the lowland-dwelling hyaena.

Hyaenas use game farms preferentially over other LUTs. This may be because these areas have lower human-predator conflict and greater food availability. Average activity levels are lowest on game farms compared to other LUTs within the 95% T-LoCoH home ranges.

Despite risks of vehicle collision, both hyaenas prefer road to non-road areas irrespective of road substrate. The lowland-dwelling hyaena crosses fast-moving tar roads on 60.91% of nights, sometimes up to seven times a night. The collar data collaborates with the high level of road mortality risk for hyaenas presented by interviewees.

Although a sample size of two collared hyaenas is too small to make definite assumptions regarding differences between hyaenas in mountains and low-lying areas, this is the first study to examine brown hyaena movement ecology in a montane environment and has the potential to act as a pilot for further research. Despite hyaenas implementing behavioural and ranging adjustments across LUTs in response to perceived threats, hyaenas still face anthropogenic threats with the threats in low-lying areas greater than at higher elevations. Therefore, mountains may offer some refuge to brown hyaenas until human-brown hyaena relationships in non-protected areas improve.

Chapter 7: Brown hyaena diet and food acquisition

7.1. Introduction

Perceived or real depredation events and the risk that predators may pose to livestock and expensive game species, often induces human-predator conflict (Boast *et al.*, 2016; Maude, 2005; Yirga Abay *et al.*, 2011). Dietary analysis quantifies the real impact of predators on livestock and game which can be used as a valuable tool for increasing understanding of predators and defining conservation management (Boast *et al.*, 2016). This chapter aims to determine brown hyaena diet, assess dietary diversity, distinguish the most important sources for acquiring food items, and link these findings to beliefs held within the community. I examine three factors – leopard dietary composition, relative abundance of prey species, and availability of commercially hunted species – to establish their effects upon brown hyaena diet.

7.1.1. Optimal foraging theory and dietary selection in carnivores

The optimal foraging theory states that the consumption of a prey species is directly linked with its availability, therefore predation becomes a process whereby the costs and benefits are equalised (Brown, 1988; Krebs, 1978). When a prey item is abundant, predators consume it more often. In areas where productivity is lower, predators increase the range of prey consumed (Krebs, 1978). Analysis of lion diets across Africa and India support the optimum foraging theory (Hayward and Kerley, 2005). The optimal foraging theory has also proved true when applied to opportunistic scavengers such as brown hyaenas (Maude, 2005). Brown hyaenas vary their diet to include more species when food availability is lower (Maude, 2005).

7.1.2. Hunting and scavenging behaviour in brown hyaenas

Despite living in social units, brown hyaenas are solitary foragers and hunters (Owens and Owens, 1978). Brown hyaenas forage in a zig-zag pattern and use their refined

sense of smell to maximize the potential to find food (Owens and Owens, 1978). Brown hyaenas are poor hunters (Mills, 1990). In the Kgalagadi Transfrontier Park, brown hyaenas were observed hunting during only 0.8% of feeding observations. Only 6% of these observations were successful and these were confined to very small prey items (Mills, 1976). This suggests that the majority of food consumed, which is primarily large mammalian remains, are scavenged rather than hunted (Owens and Owens, 1978). In pastoral areas near the Makgadikgadi National Park, radio-collared brown hyaenas were confirmed hunting only 3.7% of the time. Witnessed kills were of small mammals weighing less than 3.5 kg (Maude, 2005).

Brown hyaenas are predominantly scavengers with purloined food taken from or leftover by other predators as their main food source (Owens and Owens, 1978; Stein *et al.*, 2013). In areas where large predators are resident, brown hyaena scats contain a greater proportion of large mammal remains, indicating an increased level of scavenging (Yarnell *et al.*, 2013). Large African carnivores have a high level of dietary overlap (Hayward and Kerley, 2008). Due to this overlap and their reliance on other predators for food, brown hyaenas have a complex relationship with other large predator species (Owens and Owens, 1978). In locations where apex predators such as leopards and cheetahs are present, sufficient food for scavenging is available and brown hyaenas do not need to hunt (Slater and Muller, 2014). Brown hyaenas frequently steal kills from other carnivores. On a game reserve in South Africa's Eastern Cape Province, brown hyaenas stole kills from cheetahs during 11% of the 81 feeding observations (Slater and Muller, 2014). Brown hyaenas have been observed stealing food from large predators such as lions and leopards, and even chasing adult male leopards up trees (Mills, 2015; Owens and Owens, 1984; Owens and Owens, 1978). The leopard's submissive behaviour may be attributed to the brown hyaena's strong jaws, which could pose a fatal threat to a leopard. Additionally, the leopard's svelte body is not as well protected in a fight as the brown hyaena's strong shoulders and thick mane. A leopard may consider the loss of a meal a better alternative than a crushed leg (Owens and Owens, 1984). It is predicted that brown hyaenas in and around the Soutpansberg Mountains will acquire food from leopards on a regular basis and therefore species that occur frequently in leopard scats will also be common in brown hyaena scats (hypothesis 7.1).

In an area that was largely deficient of medium to large predators aside from caracals, brown hyaenas consumed medium sized mammals rather than large mammals (Maddock, 1993). Therefore, in areas lacking apex predators brown hyaenas may be forced to hunt to a greater extent (van der Merwe *et al.*, 2009).

7.1.3. Brown hyaena diet

Many brown hyaena dietary studies have been confined to desert areas, primarily the Kalahari and Namibian coastline (Kuhn *et al.*, 2008; Mills and Mills, 1978; Siegfried, 1984; Stuart and Shaughnessy, 1984). The closest environment to my study area where scat analysis has been conducted is the Waterberg region of Limpopo Province (Burgener and Gusset, 2003; Ramnanan *et al.*, 2016) and farmlands and protected areas in North West Province (van der Merwe *et al.*, 2009). However, these studies are only based on small sample sizes of 38, 31, and 42 scats respectively, and the habitats and animal species present vary somewhat from my study site (Burgener and Gusset, 2003; Ramnanan *et al.*, 2016; van der Merwe *et al.*, 2009).

Brown hyaenas have a catholic diet (Burgener and Gusset, 2003; Mills and Mills, 1978; Owens and Owens, 1978). A wide variety of species are often detected in dietary studies (Mills, 1990; Owens and Owens, 1978; Slater and Muller, 2014). Fifty-eight different species were found in scats collected over two years in the central Kalahari (Owens and Owens, 1978). In the Shamwari Game Reserve in the Eastern Cape Province, brown hyaenas consumed at least 14 mammal species (Slater and Muller, 2014). In Mankwe Wildlife Reserve and Pilanesberg National Park, brown hyaena scats contained 21 different food items (Yarnell *et al.*, 2013). Invertebrates have been detected at many study sites (Burgener and Gusset, 2003; Mills and Mills, 1978; Owens and Owens, 1978; Slater and Muller, 2014; Stuart and Shaughnessy, 1984; Yarnell *et al.*, 2013). These may be deliberately consumed, but another plausible alternative is that they are ingested while feeding from carcasses (van der Merwe *et al.*, 2009). Plant materials are commonly found in brown hyaena scats (Burgener and Gusset, 2003; Owens and Owens, 1978; Slater and Muller, 2014; Stuart and Shaughnessy, 1984; van der Merwe *et al.*, 2009) and can play an important role in

meeting animals' moisture needs in arid environments (Owens and Owens, 1978). In the Kgalagadi Transfrontier Park, 29% of all foods eaten are wild fruits with a particular preference for tsama melons and gemsbok cucumbers (Mills, 1982a). Additionally, reptiles can contribute to their diet and brown hyaenas have been observed killing tortoises (Slater and Muller, 2014). Based on previous studies confirming variability in brown hyaena diet and the high mammalian biodiversity at the study site, I expect to find a wide variety of species within the brown hyaena scats (hypothesis 7.2). I predict that brown hyaena diet will correlate with species abundance within the study area (hypothesis 7.3).

When a particular food source is very readily available, the breadth of the brown hyaena's diet lowers. Along the Namibian coast, brown hyaenas predominantly eat cape fur seals (*Arctocephalus pusillus pusillus*) (Kuhn *et al.*, 2008; Siegfried, 1984; Skinner *et al.*, 1995; Stuart and Shaughnessy, 1984; Wiesel, 2006). In this area, hunting is more prevalent than scavenging with instances of mass killing and non-consumption recorded during times when seal pups are plentiful (Wiesel, 2006; Wiesel, 2010).

Brown hyaena diet is affected by land use type (LUT). In the Makgadikgadi National Park, brown hyaenas primarily consume large endemic animals such as zebra. In neighbouring pastoral land, hyaenas rely upon livestock carcasses (Maude, 2005). In lean and peak seasons, brown hyaenas resident in the national park broaden their diet to incorporate a wider variety of species while those living in pastoral areas maintain a similar diet year round (Maude, 2005).

Many carnivores adapt to live close to urban areas and exploit anthropogenic food sources including bears, wolves, red foxes (*Vulpes vulpes*), coyotes, raccoons, and Eurasian badgers (*Meles meles*) (Bateman and Fleming, 2012). Spotted, striped, and brown hyaenas are able to survive in areas around villages and towns (Bateman and Fleming, 2012; Kuhn, 2014; Yirga *et al.*, 2013). Analysis of 211 scats from spotted hyaenas living in close proximity to people in northern Ethiopia showed that domesticated prey composed 99% of their diet. Only three scats contained hairs from native wild species (Yirga *et al.*, 2013). Spotted hyaenas alter their feeding behaviour in relation to Christian fasting periods. Prior to the fasting period, spotted hyaenas

predominantly scavenge on discarded human foods, however once the fasting period began, they adapt to actively hunt donkeys (Yirga *et al.*, 2012). The brown hyaena's wide and opportunistic diet, secretive nature, and low water requirements have enabled the species to survive in human-dominated areas where less adaptable carnivores cannot persist (Maude, 2005). Human-dominated farmlands offer a number of feeding advantages to brown hyaenas. Livestock or game carcasses which died from disease, starvation, old age, or predation present scavenging opportunities for brown hyaenas (Maude, 2005). Organic remains of human food are frequently disposed of in human-dominated areas and can offer an alternative food source for scavengers (Maude, 2005). Brown hyaenas have been observed consuming human refuse along the Namibian coastline as well (Skinner *et al.*, 1995).

Commercial hunting outfitters often process carcasses at abattoirs on site. Remains from this process are placed in vulture restaurants for scavengers to clear. Vulture restaurants in South Africa have a positive effect on brown hyaena and black-backed jackal abundance (Yarnell *et al.*, 2014). Hunting clients pay for animals that are wounded during the hunting process on the assumption that the animal will die (B. Botha, pers. comm.). It is predicted that species that are commonly sold in commercial hunts will comprise a large proportion of the brown hyaena diet in this study because remains left in vulture restaurants and carcasses of fatally wounded animals present easy scavenging opportunities (hypothesis 7.4).

7.1.4. Consumption of domestic animals by brown hyaenas

Large carnivores show a preference for wild prey over livestock, even in areas where livestock is abundant and easier to catch (Biswas and Sankar, 2002; Selvan *et al.*, 2013; Valiex *et al.*, 2012). However as a scavenger, it is difficult to ascertain with certainty whether this statement is applicable to brown hyaenas. In the majority of studies, brown hyaenas consume livestock either infrequently (Maude and Mills, 2005; Stein *et al.*, 2013) or not at all (Mills and Mills, 1978; Owens and Owens, 1978; Ramnanan *et al.*, 2016; Siegfried, 1984). In a study of 212 brown hyaena scats and 44 den orts on Namibian farmlands, only 28 samples contained evidence of domestic livestock (Stein

et al., 2013). The most commonly consumed livestock were calves (Stein *et al.*, 2013). In fifteen years of observations, no instances of livestock consumption by brown hyaenas were observed in one area of the northern Transvaal (Skinner, 1976). However in another region of the same province, a large male hyaena killed 130 sheep over a four month period (Skinner, 1976). These varied reports and evidence of predation problems ceasing after the removal of a problematic brown hyaena which has learned to mass hunt easy prey, suggest that this behaviour is associated with rogue individuals rather than ingrained across whole clans (Skinner and Chimimba, 2005; Weise *et al.*, 2015).

Although scat analysis reveals diet and consequently predator-prey interactions, a weakness of this methodology is it offers little information about the predation process or how the food was collected (Mills and Mills, 1978; Nilsen *et al.*, 2012). Although it is possible to quantify the prevalence of domestic animals in the brown hyaena diet, it is difficult to conclusively determine whether livestock is hunted or scavenged. Based on observational studies of brown hyaenas, the most likely explanation for brown hyaena tracks or direct observations near livestock remains is hyaenas are scavenging on a carcass that had died either of natural causes or predation by another carnivore (Maude, 2005; Skinner, 1976). Direct observations of brown hyaenas inhabiting farmland show no indication of brown hyaenas hunting livestock, despite carcasses of livestock composing the largest percentage of their diet in farming land adjacent to the Makgadikgadi National Park (Maude, 2005). Based on reports from interviewees, the large distances travelled by brown hyaenas, and their opportunistic feeding behaviour, I expect to find livestock in the scats but at a low level (hypothesis 7.5).

Despite frequent persecution by farmers, the benefits that farmland offer such as a secure source of food throughout all seasons, outweigh the risks for brown hyaenas (Kent and Hill, 2013; Maude, 2005). On rare occasions, this is not the case depending on the level of persecution experienced (Ogada *et al.*, 2003). The importance of farmland for brown hyaena survival and conservation was first suggested in the mid 1970s and 1980s (Skinner, 1976; Stuart *et al.*, 1985) and since then further evidence has supported this theory (Kent and Hill, 2013). Other large carnivores are also

succeeding on farmlands including jaguars (Boron *et al.*, 2016) and African wild dogs (Ramnanan *et al.*, 2013), indicating the importance of non-protected areas for carnivore conservation.

7.2. Methods

7.2.1. Scat analysis

Scat analysis is the most commonly used method to determine the diets of terrestrial carnivores (Klare *et al.*, 2011) and is one of the most accurate methods if correctional indexes are applied (e.g. Ackerman *et al.*, 1984) as it does not underestimate the smaller prey items in the same way that direct observation can and accounts for unrecognisable prey items (Davies-Mostert *et al.*, 2010; Mills and Mills, 1978). Scat detecting dogs can be used to locate samples (MacKay *et al.*, 2008a) or researchers can collect scats opportunistically (Chase Grey, 2011; Mbizah *et al.*, 2012; van der Merwe *et al.*, 2009), as was done in this study. Researchers' movements limit opportunistic collection and consequently samples are not collected evenly across a study area (Burgener and Gusset, 2003). As humans frequently travel on roads, this may mean that more scats are collected along these corridors (Mbizah *et al.*, 2012). Brown hyaenas frequently utilise road and trail systems (Hulsman *et al.*, 2010; Thorn *et al.*, 2011a), which helps to negate this bias. No behavioural ramifications or negative effects have been recorded in study species following the removal of scats (Mackay *et al.*, 2008b).

Brown hyaena scats were collected most frequently by the side of drivable roads or at den sites. The majority of scats were collected in the dry winter months. During this time, there were no rains washing away the samples or competition from dung beetles (*Scarabaeus zambesianus*). It was not possible to age the scats but it was assumed that most scats were less than six months old and postdated the previous rainy season.

Brown hyaena scats were predominantly collected in the western Soutpansberg Mountains, with 70% of all analysed scats found in a 10 km radius from the geographic

centre of the property Lajuma (Figure 7.1). The remaining 30% of analysed faecal samples were found in the Limpopo Valley and lowveld. No known studies of brown hyaena diet have been conducted in this area.

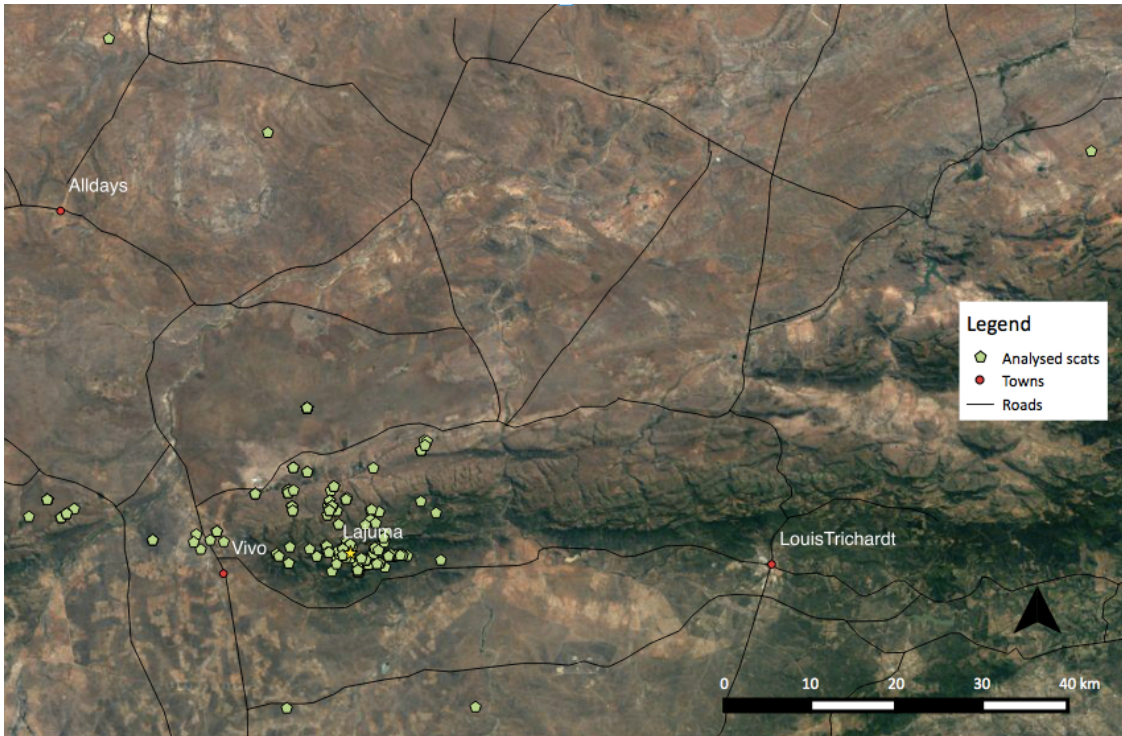


Figure 7.1 Map of analysed brown hyaena scat collection locations in and around the Soutpansberg Mountains. Roads indicate tarred roads.

Scats were either collected at latrine sites with accumulations of multi-aged faeces or as a singular cluster from one occasion (Figure 7.2). Brown hyaenas will commonly utilise latrine sites as an olfactory territorial marker (Hulsman *et al.*, 2010). Latrines are often situated at the side of roads and at important landmarks such as junctions and rivers (Hulsman *et al.*, 2010). Many of the latrines that were discovered during this study were located at crossroads. If the scat was part of a latrine site, scats were bagged together by age as determined by visual comparison and spacing.



Figure 7.2 a. Brown hyaena scat is often white and consists of several small, heavy, roundish balls. They are sometimes found in singular piles. b. Hyaenas will frequently defecate in a latrine.

Brown hyaena scats were visually identified by their size, chalky-white colouration when dry, and shape (Figure 7.2a). Within the study site, scats of two other predators could be confused with brown hyaena scats. Leopard scats often have a brownish-green colouration and an elongated shape as opposed to round ball-shaped brown hyaena scats (Stuart and Stuart, 2003). Leopard scats are also lighter in weight than brown hyaena scats. Spotted hyaenas are present within the study site, but are seen infrequently. Spotted hyaena scat is very similar in appearance to brown hyaena scat and can be easily confused (Mills and Hofer, 1998). Both species have strong dentition designed to crush bones and both are able to digest bone fragments due to hydrochloric gastric acids (Estes, 1991; Mills, 1990; Sutcliffe, 1970). Consequently, the colouration of scat from brown and spotted hyaenas is indistinguishable. Size is the defining difference between the two species' scats. Spotted hyaena scats are considerably larger and heavier, weighing about three times more than the brown hyaena scats (Stuart and Stuart, 2003).

Scats were collected in resealable plastic bags to avoid cross contamination (Yirga *et al.*, 2013). The date, global positioning system (GPS) location, altitude, and species were recorded. Upon collection scats were visually identified and labeled in the field. Oldrich van Schalkwyk, an experienced Field Guide Association of South Africa field guide, subsequently inspected the scats individually. Any scats that yielded a

discrepancy between the original and later species designation were excluded from the study to ensure accuracy. I removed 25 samples from the study on this basis.

Scat samples were carefully washed with lukewarm water in a wire sieve with 1 mm sized mesh (Kuhn *et al.*, 2008; Ramnanan *et al.*, 2013; van Dijk *et al.*, 2007). Washing removed all faecal matter from the sample leaving only hair, bones, and other organic matter. The remaining material was placed on trays lined with newspaper and left in a tent for several days to dry in the sun. Once dry, the samples were rebagged for analysis.

I used hair samples to identify species consumed to the lowest possible taxonomic classification. Hair is resilient to decomposition (Chang *et al.*, 2005; Taru and Backwell, 2013) and enzymatic digestion (Lubec *et al.*, 1987; Lubec *et al.*, 1994). Although it is possible to identify species from bone fragments, it is much more challenging and less conclusive at a species level (Chase Grey, 2011; van Dijk *et al.*, 2007).

I spread the washed scat sample evenly across a random sampling tray consisting of either 36 or 100 numbered squares depending on the size of the sample (Martins *et al.*, 2011). I randomly selected 20 squares by picking numbers blindly from a bag, and two hairs were extracted from each chosen square. If several hairs were present within one square, hairs for sampling were selected based on individual characteristics. An overall representative sample of hairs was required from each scat in case more than one species was present in the scat. Hairs were inspected visually and chosen based on their visual differences to ensure that I included at least one hair of each size, thickness, shape, colour, and length in the analysis (Davies-Mostert *et al.*, 2010; Maude, 2005).

Each species' hair has a unique structure both internally from the cross-section (Figure 7.3) (Douglas, 1989) and externally from the cuticular pattern (Figure 7.4) (Keogh, 1983). Hairs also vary macroscopically by colouration, length, or thickness and although this can be a useful starting point for identifying species (Martins *et al.*, 2011), it is not as definitive as microscopic examination. Notes on the macroscopic properties of hairs were taken from all selected hairs within each scat. Macroscopic

observations from bones or other matter were also recorded. By combining macroscopic observations with cuticular prints and cross-sections, I reduced inaccuracies in species identification and all mammalian species consumed should have been discernable.

I used 20 of the selected hairs for cuticular scale imprints using methods described by Keogh (1983). Glass microscope slides were thinly covered in liquid gelatin combined with food colouring and the hairs were placed vertically into the gelatin. Once the gelatin dried, the hairs were removed and an imprint of the cuticular pattern remained (Figure 7.3). I examined these prints under a microscope at 40x magnification and compared them to prints of hairs from known species, which were created using the same technique.

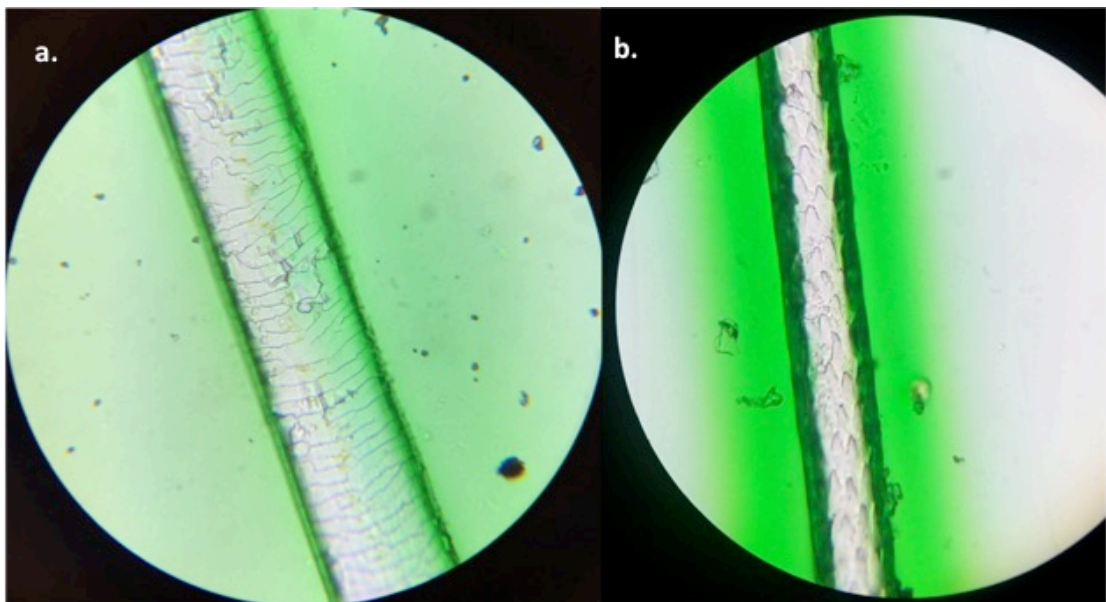


Figure 7.3 Cuticle prints at 40x magnification. a. Cuticular print from a common duiker hair. b. Cuticular print from a large spotted genet hair.

I used the remaining 20 hairs for cross-sectional examination using methods adapted from Douglas (1989). Five hairs were placed in the end of four 5.5 ml plastic Pasteur pipettes. Clear candle wax was melted until liquefied. Clear wax prevents the blockage of light from the microscope upon examination (Douglas, 1989). Liquid wax was sucked into the pipette until the hairs were fully covered. Careful manipulation of the pipette reduced the presence of air bubbles. The pipette was dipped in cold water to

speed the wax hardening. The hardened pipette was sliced into very fine discs (~ 0.2 mm) from the bottom upwards using a scalpel (Davies-Mostert *et al.*, 2010). Discs contained cross-sections of the hair samples and these were placed on a glass slide for microscopic examination of the size and shape of the medulla and cortex (Figure 7.4). I compared each sample under a microscope at 20x and 40x magnification with similarly produced slides made from reference materials.

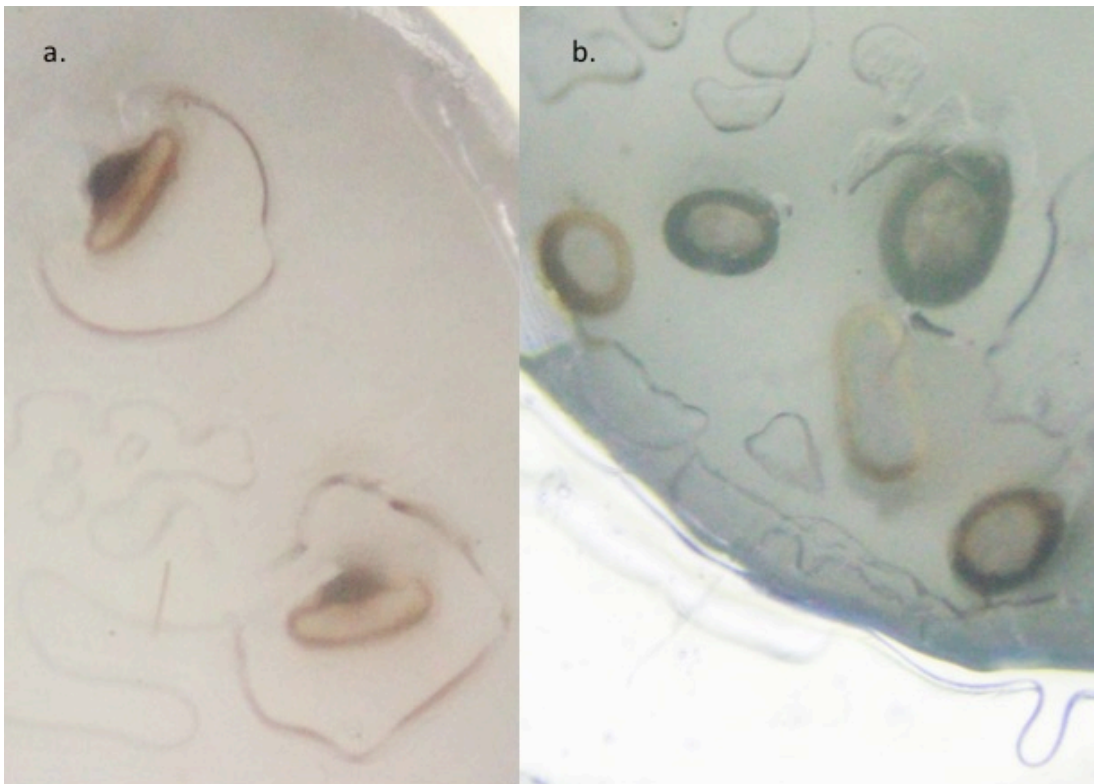


Figure 7.4 Cross-sections at 20x magnification. a. Cross-sections from impala hairs. b. Cross-sections from giraffe hairs.

A reference library was created featuring 76 hair samples from locally present mammal species, both wild and domestic. I collected these samples from carcasses of road kill, taxidermists, museum collections, and opportunistic live captures of small and large mammals. Although the structure of the hair remains similar across the species, visual differences can be seen in hair taken from different parts of the body (Bhattarai and Kindlmann, 2012). Whenever possible, I collected reference hairs from two areas on the animal's body (Davies-Mostert *et al.*, 2010). Guard hairs, which share characteristics of longer, courser body hairs, were taken interscapularly. Softer, shorter under-hairs were collected from the stomach. I used publications that include

photographs of hair structure from southern African mammals for identification in addition to the physical reference library (Keogh, 1983; Seiler, 2010; Taru and Backwell, 2013).

7.2.2. Data analysis

Diet composition

All occurrences of a prey item were calculated as a relative frequency of occurrence and a corrected frequency of occurrence (CFO) (Braczkowski *et al.*, 2012; Henschel *et al.*, 2005; Swanepoel, 2008). Relative frequency of occurrence was expressed as a percentage and was calculated as the number of times a prey species occurred, divided by the total number of occurrences, and multiplied by 100 (Alam and Khan, 2015; Ott *et al.*, 2007; Ramnanan *et al.*, 2013; Yirga Abay *et al.*, 2011). I employed CFO to account for occasions when more than one prey item was found in a scat. For example, if there was two species in one scat, each species occurrence was weighted as 0.5 (Henschel *et al.*, 2005; Karanth and Sunquist, 1995). I transformed the cumulative corrected occurrences into a frequency of occurrence using the method described for ascertaining relative frequency of occurrence. I used corrected occurrences or CFOs in all analyses and comparisons.

Although relative frequency of occurrence and CFO creates comparable results, it fails to account for prey size or the likelihood of leaving remains (Klare *et al.*, 2011). The consumption of small prey is linked to a higher production of scats produced per unit mass of prey consumed (Bhattarai and Kindlmann, 2012). An overestimate can materialise in the number of small prey species consumed and this is frequently corrected for in scat studies of carnivores by employing a correction factor (Ackerman *et al.*, 1984; Boast *et al.*, 2016; Davies-Mostert *et al.*, 2010; Marker *et al.*, 2003b; Wachter *et al.*, 2012). The employment of a correction factor is recommended in large carnivore scat analysis to reduce the bias in the different digestion rates required to process various sized prey (Klare *et al.*, 2011; Wachter *et al.*, 2012). However, a correction factor was not employed because no correction factor has been developed

for any hyaenid species (Klare *et al.*, 2011). Additionally, as a scavenger a correction factor may not be entirely appropriate in brown hyaena scat analysis (B. Wachter, pers. comm.). Correction factors are designed for species that eat the entirety or the majority of a prey animal (Wachter *et al.*, 2012) rather than animals which have an opportunistic and piecemeal approach to consumption like the brown hyaena.

If an applicable correction factor is not available, biomass calculation methods based on volume and mass of species found within scats are recommended (Klare *et al.*, 2011). This method acknowledges the relative volume or weight of material from each prey species' in relation to the entire sample (Klare *et al.*, 2011). This was not possible to employ because there was a high incidence of multiple species per scat and because of the presence of smaller species. When multiple species are found in one scat, it is not feasible to segregate the contents into weighable species-specific masses. In addition, tiny rodent hairs could not be washed as thoroughly as longer hairs from larger mammals because they would fall through the sieve. Therefore, I deliberately left a small amount faecal matter embedded in clumps on rodent hairs during the washing process. The remaining faecal matter was removed from hairs selected for microscopic examination using a mortar and pestle but it would be extremely challenging to remove all faecal matter from the entire sample in a similar fashion. If left, the presence of this faecal matter would affect mass-based calculations. As a consequence, although there are limitations to using frequencies of occurrence to analyse scat contents, I decided that there was no viable alternative. Thus, I selected frequency of occurrence and CFO as the primary means of presenting results from brown hyaena scats.

Dietary diversity

The Brillouin index was used to calculate dietary diversity within brown hyaena scats following this equation (Brillouin, 1956):

$$H = \frac{\ln N! - \sum \ln n_i!}{N}$$

H is the diversity, N is the total number of prey occurrences, and n_i indicates the total number of prey items found for the i th species (Brillouin, 1956; Glen and Dickman, 2006). Cumulative dietary diversity (H_k) was plotted against the number of scats analysed (k) following Glen and Dickman (2006) to determine whether an adequate number of scats were sampled.

Diet composition and species abundance

I tested corrected frequency of occurrence in scats against relative species abundance. I collected 79.51% of scats within the area sampled during the 2014 spatially explicit capture recapture (SECR) camera trapping survey or up to 3 km from the boundary. This subsection of scats was tested against the relative abundance index (RAI) of species from the 2014 SECR camera trapping survey. I excluded scats collected outside of the camera trapping area in this analysis. I determined species abundance using RAI as described in section 5.3.3.2. RAI for species found in scats was converted into a proportion and following Braczkowski *et al.* (2012), proportional abundance was tested against prey consumption to determine prey preference. The Jacobs' index was used to assess prey preference (Jacobs, 1974):

$$D = \frac{r_i - p_i}{r_i + p_i - 2r_i p_i}$$

where r_i is the proportion of prey species i consumed as determined by CFO and p_i is the proportional abundance of prey species i from the RAI value. I excluded flying birds and very small mammals (average weight <1 kg) because of their low detection frequencies on camera traps (Braczkowski *et al.*, 2012; Henschel *et al.*, 2005). Only prey species that occurred in the scats were included to avoid biasing results through the inclusion of unconsumed species (Yarnell *et al.*, 2013). Linear regression in R v 3.2.3 (R Development Core Team, 2016) determined if a relationship between the abundance of species and their occurrence in scats existed.

Diet composition and commercial hunting prevalence

I obtained data on all animals commercially hunted or wounded on four large commercial hunting farms (between 512 ha and 3,000 ha) within the vicinity of the western Soutpansberg Mountains in 2014 and 2015. These data were merged to give a per species frequency of hunting. Collated hunting data was tested against corrected species occurrence in brown hyaena scats collected in 2014 and 2015 using a Spearman's Rank Correlation test in R v 3.2.3 (R Development Core Team, 2016). Hunting levels controlled for abundance were tested for correlation with corrected species occurrence in hyaena scats using a Spearman's Rank Correlation test. The number of animals hunted per species was divided by the RAI of the species. RAI was computed from the 2014 SECR camera trapping survey.

I tested seasonal variation in scat contents between hunting and non-hunting seasons. Hunting season is typically defined as May 1st to September 30th. However to account for a delay in any hunting-related effects registering in the faeces, I categorised scats collected between May 15th and October 15th as occurring in hunting season and scats collected between October 16th and May 14th as occurring in non-hunting season. I tested rates of species occurrences in scats between hunting and non-hunting seasons for significant difference using a Wilcoxon signed rank test in R v 3.2.3 (R Development Core Team, 2016).

A comparison of leopard diet and brown hyaena diet

I examined overlap between the leopard and the brown hyaena diet to determine the likelihood of brown hyaenas relying upon the only other permanent apex predator present for food. Information on the contents of 162 leopard scats from Fitzgerald (2015) was merged with data on the composition of 75 leopard scats from Sheppard (2016). Initially I compared data from 237 leopard scats collected between 2011 and 2015 in the western Soutpansberg Mountains with the 288 brown hyaena scats analysed. Leopard scats were analysed using the same methodologies described in section 7.2.1. I compared leopard diet with brown hyaena diet for dietary overlap using the Pianka's index (Pianka, 1973):

$$\alpha = \frac{\sum P_{ia}P_{ib}}{\sqrt{\sum P_{ia}^2 \sum P_{ib}^2}}$$

where α equals the dietary overlap between species a and species b , P_{ia} is corrected frequency of occurrence in species a , and P_{ib} is corrected frequency of occurrence in species b . The index ranges between 0 (no overlap) and 1 (complete overlap) with values greater than 0.6 considered biologically significant (Navia *et al.*, 2007; Pianka, 1973). Due to the wider collection area for brown hyaena scats, I conducted a second calculation comparing all leopard scats ($n = 237$) with all brown hyaena scats collected within 10 km of the central point on the property Lajuma ($n = 202$). The Wilcoxon signed rank test in R v 3.2.3 (R Development Core Team, 2016) tested for a significant difference between the corrected occurrences of species found within the leopard and the brown hyaena diets.

7.3. Results

7.3.1. Dietary diversity

Consumption at a species level was ascertained for 288 of the 311 scats collected (92.6%). Seventy-five per cent of all consumed animal species were detected after analysing 84 scats (Figure 7.5). The species accumulation curve reaches asymptote after analysing approximately 100 samples suggesting that a representative sampling of the diet was achieved. All mammalian and avian prey species consumed by brown hyaenas were detected after analysing 279 faeces.

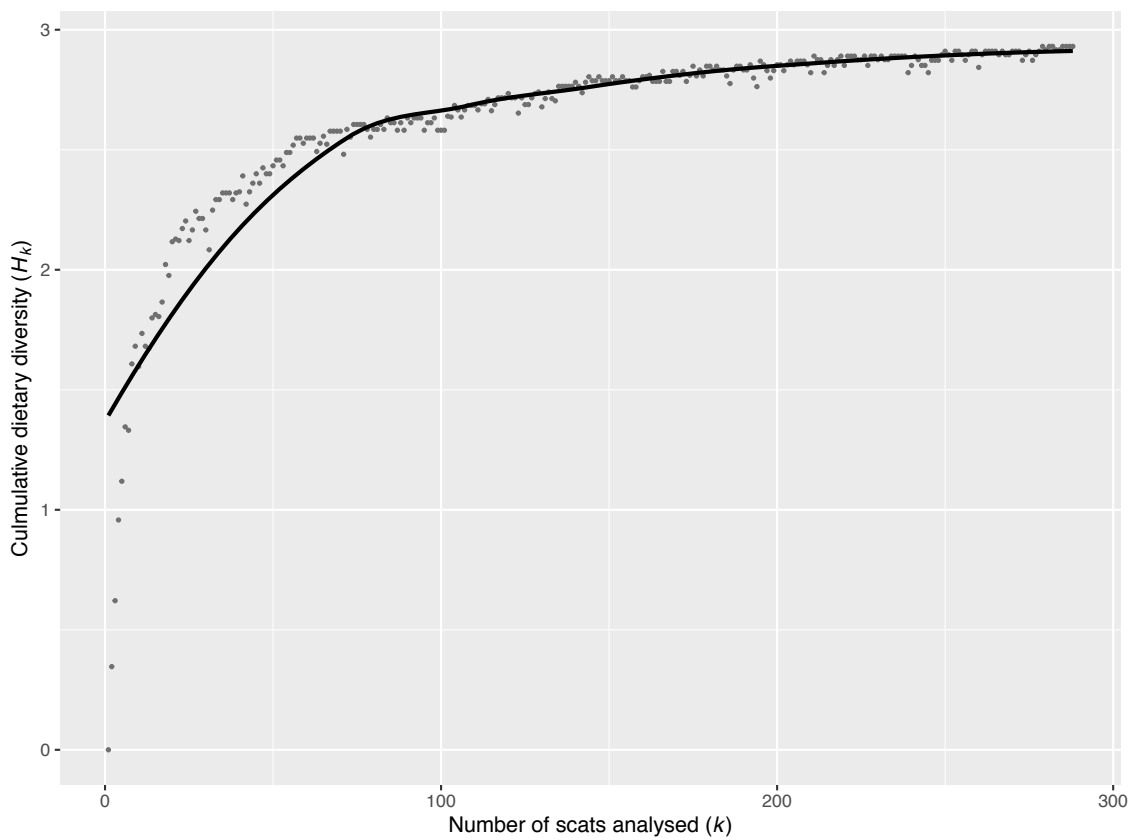


Figure 7.5 Cumulative dietary diversity of brown hyaenas (H_k) in and around the Soutpansberg Mountains in relation to the number of scats analysed (k).

The diversity of prey occurrences in brown hyaena scats (H) is calculated at 2.93 using the Brillouin index.

7.3.2. Diet composition

Within an individual scat, a variety of species was often detected (mean 1.95 species \pm 0.91 S.D.; range 1 - 5 species per scat) (Table 7.1).

Table 7.1 Number of mammalian and avian species identified per brown hyaena scat collected in and around the Soutpansberg Mountains.

	Number	Percentage
Scats with one species	107	19%
Scats with two species	104	18.47%
Scats with three species	62	11.01%
Scats with four species	13	2.31%
Scats with five species	2	0.36%

Within the 288 identifiable scats, all animal contents were classifiable to a species level aside from invertebrates and mongoose species. All occurrences containing mongoose hair from any of the five species present across the study site are referred to as mongoose. Forty-seven mammal species (including mongoose) were distinguished from hairs and one avian species (ostrich) was identified from feather composition (Table 7.2). Two scats contained unidentifiable invertebrate remains. Plant material including leaves, grass, and seeds were found in 22 scats. It was not possible to ascertain plant species. A piece of hard plastic was found in one scat.

Because of the frequency of multiple species per scat, 563 prey item occurrences were recorded. Based on CFO, the most frequently consumed species is common warthog (10.32%) (Table 7.2). Bushbuck is the second most commonly consumed species (9.81%). Impala comprises 8.82% of the diet and chacma baboon is found in 6.86% of the total samples. Other regularly occurring species include common duiker (5.97%), bushpig (5.61%), greater kudu (5.12%), goat (4.89%), nyala (3.33%), and vervet monkey (*Chlorocebus pygerythrus*) (3.24%).

Table 7.2 Species consumed by brown hyaenas in and around the Soutpansberg Mountains. Data ordered by corrected frequency of occurrence.

Species	Taxonomic order*	Size group for prey**	Occurrences	Relative frequency of occurrence (%) (n=563)	Corrected frequency of occurrence (%) (n=288)
Common warthog	Cetartiodactyla	Large	72	12.79	10.32
Bushbuck	Cetartiodactyla	Medium ¹	45	7.99	9.81
Impala	Cetartiodactyla	Medium	57	10.12	8.82
Chacma baboon	Primates	Medium	42	7.46	6.86
Common duiker	Cetartiodactyla	Medium	31	5.51	5.97
Bushpig	Cetartiodactyla	Large ¹	39	6.93	5.61
Greater kudu	Cetartiodactyla	Large	25	4.44	5.12
Goat	Cetartiodactyla	Large ²	24	4.26	4.89
Nyala	Cetartiodactyla	Large	13	2.31	3.33
Vervet monkey	Primates	Small	18	3.2	3.24
Red duiker	Cetartiodactyla	Small	14	2.49	3.18
Cow	Cetartiodactyla	Large ³	16	2.84	2.92
Waterbuck	Cetartiodactyla	Large	13	2.31	2.04
(<i>Kobus ellipsiprymnus</i>)					
Samango monkey	Primates	Small	9	1.6	1.94
Mongoose	Carnivora	Small ⁵	7	1.24	1.81
Gemsbok (<i>Oryx gazella</i>)	Cetartiodactyla	Large	9	1.6	1.77
Yellow spotted dassie	Hyracoidea	Small	8	1.42	1.77
(<i>Heterohyrax brucei</i>)					
Blesbok	Cetartiodactyla	Large	8	1.42	1.71
African civet	Carnivora	Small	10	1.78	1.62
Sheep	Cetartiodactyla	Large ⁴	11	1.95	1.53
Brown hyaena	Carnivora	Medium ¹	9	1.6	1.39
Giraffe	Cetartiodactyla	Large	7	1.24	1.27
Black-backed jackal	Carnivora	Small	6	1.07	1.22
Aardvark	Tubulidentata	Medium	6	1.07	1.16
Steenbok	Cetartiodactyla	Small	6	1.07	1.04
Zebra	Perissodactyla	Large	6	1.07	0.97
House rat	Rodentia	Very Small ¹	7	1.24	0.9
(<i>Rattus rattus</i>)					
Eland	Cetartiodactyla	Large ¹	3	0.53	0.81
(<i>Taurotragus oryx</i>)					
Four striped mouse	Rodentia	Very Small	3	0.53	0.64
(<i>Rhabdomys pumilio</i>)					
Sable	Cetartiodactyla	Large	3	0.53	0.64
Rock dassie	Hyracoidea	Small	4	0.71	0.58
(<i>Procavia capensis</i>)					
Gambian giant rat	Rodentia	Small	2	0.36	0.43
(<i>Cricetomys gambianus</i>)					

Species	Taxonomic order*	Size group for prey**	Occurrences	Relative frequency of occurrence (%) (n=563)	Corrected frequency of occurrence (%) (n=288)
Lesser red musk shrew (<i>Crocidura hirta</i>)	Eulipotyphla	Very Small	3	0.53	0.43
Rock elephant shrew (<i>Elephantulus myurus</i>)	Macroscelidea	Very Small	3	0.53	0.43
Blue wildebeest	Cetartiodactyla	Large	3	0.53	0.41
Ostrich	Struthioniformes	Large ⁶	3	0.53	0.36
Bat-eared fox (<i>Otocyon megalotis</i>)	Carnivora	Small	1	0.18	0.35
Caracal	Carnivora	Small	1	0.18	0.35
Lesser bushbaby (<i>Galago senegalensis</i>)	Primates	Very Small	1	0.18	0.35
Sharpe's grysbok (<i>Raphicerus sharpei</i>)	Cetartiodactyla	Small	1	0.18	0.35
Large spotted genet	Carnivora	Small	2	0.36	0.29
Swamp musk shrew (<i>Crocidura mariquensis</i>)	Eulipotyphla	Very Small	2	0.36	0.29
Klipspringer (<i>Oreotragus oreotragus</i>)	Cetartiodactyla	Small	3	0.53	0.27
Cape porcupine	Rodentia	Small	2	0.36	0.23
Red hartebeest (<i>Alcelaphus buselaphus</i>)	Cetartiodactyla	Large	2	0.36	0.23
Domestic dog	Carnivora	Small ⁷	1	0.18	0.17
Small spotted genet	Carnivora	Small	1	0.18	0.12
Red veld rat (<i>Aethomys chrysophilus</i>)	Rodentia	Very Small	1	0.18	0.09

*From the International Union for Conservation of Nature (2015).

**Based upon average adult female weights and groups given by Mills and Mills (1978). Very small < 1 kg, Small 1 - 15 kg, Medium 15 - 50 kg, Large >50 kg. Average adult female weights from Skinner and Chimimba (2005) unless superscripted numbers indicate an alternative reference.

¹ From Stuart and Stuart (2007).

² Based on Boerbok female average (J. Steyn, pers. comm.).

³ Average of heifer weights for Bonsmara, Nguni, and Heugonot breeds (SA Studbook, 2013).

⁴ Based on Dorper sheep female for 6 teeth + (Dorper Sheep Breeders' Society of South Africa, 2016).

⁵ Average weight of all mongoose photographed in occupancy survey (dwarf mongoose, slender mongoose, banded mongoose, water mongoose, and Selous' mongoose).

⁶ From Hockey *et al.* (2005).

⁷ Average weight for a mongrel (Evans and De Lahunta, 2013).

The taxonomic order Cetartiodactyla accounts for 72% of all prey occurrences (Figure 7.6). Eight of the ten most commonly consumed species are in the order Cetartiodactyla. This order includes 22 ungulate species, accounting for almost half of the mammalian species diversity recorded. Primates are the second most commonly consumed order of species, accounting for 13% of all occurrences. Carnivore species comprise 7% of all prey occurrences. Nine carnivore species were found, although this would undoubtedly be higher if mongooses could be identified at a species level. Brown hyaena hair is detected in 1.39% of corrected occurrences.

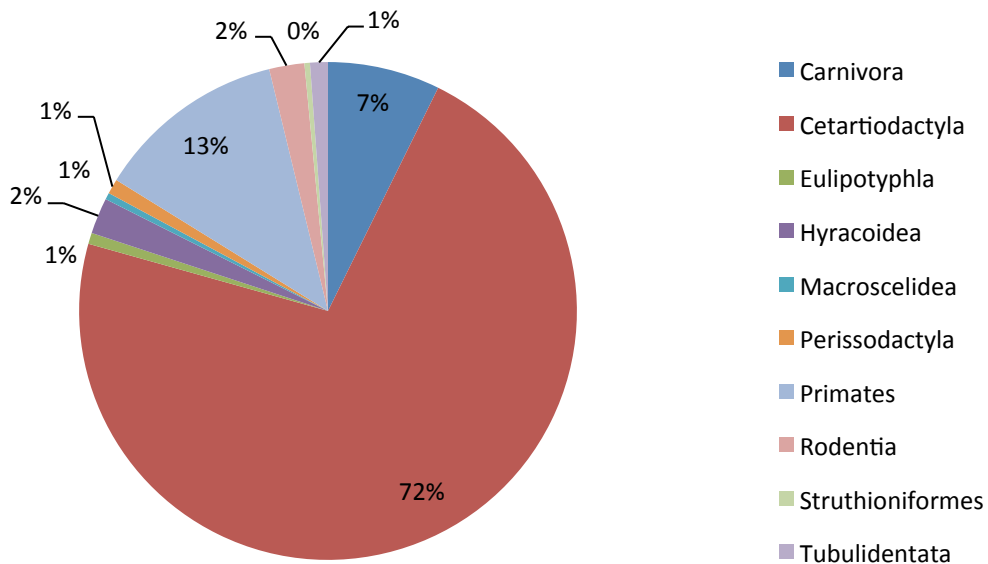


Figure 7.6 Percentage of occurrences by taxonomic order in brown hyaena scats collected in and around the Soutpansberg Mountains.

Medium and large sized animals occur the most frequently (Figure 7.7). Large animals greater than 50 kg comprise 44% of the diet while medium animals weighing between 15 and 50 kg account for 34% of the diet. Very small animals weighing less than 1 kg are infrequently consumed (3%).

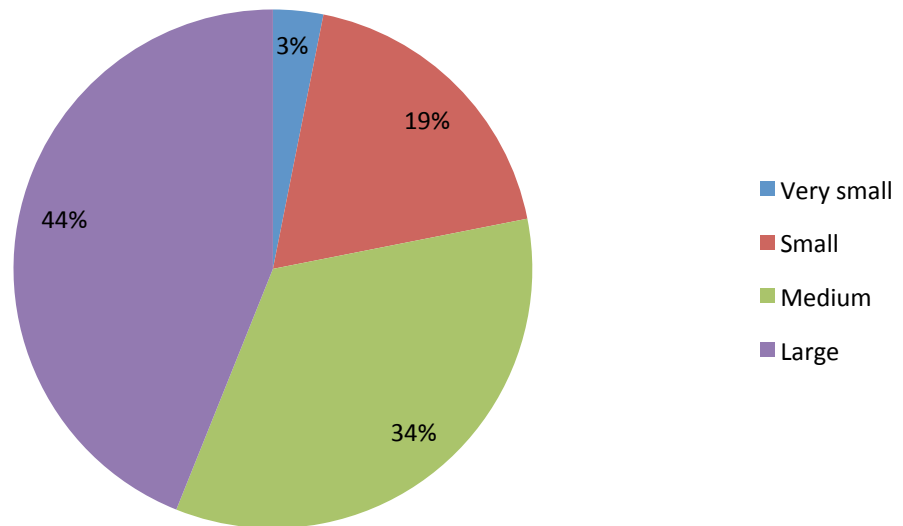


Figure 7.7 Percentage of occurrences by size of prey order in brown hyaena scats collected in and around the Soutpansberg Mountains.

Domestic animals contribute to the brown hyaena diet, however native game species play a more important dietary role. Collectively cows, goats, and sheep were recorded on 26.92 corrected occasions, equating to 9.35% of all dietary occurrences. Domestic dog was only recorded on one occurrence.

7.3.3. Diet composition and species abundance

Relative species abundance was calculated from the 2014 SECR camera trapping survey data. Sixty-one species of mammals and birds were photographed during the 47-day camera trapping survey. This includes five different mongoose species. It is not possible to differentiate between rock dassie and yellow-spotted dassie from the camera trap photos, therefore the category dassie is used to encompass both species.

Thirty-three species detected on the cameras were found in the scats (Table 7.3). Species which were photographed by the camera traps but do not occur in the scats include bird species, bats, leopard, spotted hyaena, honey badger, white rhinoceros (*Ceratotherium simum*), horse (*Equus caballus*), ground squirrel (*Xerus inauris*),

donkey, scrub hare (*Lepus saxatilis*), Jameson's red rock rabbit (*Pronolagus randensis*), domestic cat (*Felis catus*), and African buffalo (*Syncerus caffer*). The most abundant species is the cape porcupine, with chacma baboon, bushbuck, greater kudu, and giraffe the next most abundant species according to the camera trap data.

Table 7.3 Relative abundance index (RAI) of species found in brown hyaena scats from a 220 km² area in the western Soutpansberg Mountains. Based on sampling using camera traps between August and October 2014 and ranked by RAI (%).

Species	Number of capture events*	RAI	RAI (%)
Cape porcupine	464	987.23	12.91
Chacma baboon	367	780.85	10.21
Bushbuck	312	663.83	8.68
Greater kudu	274	582.98	7.62
Giraffe	237	504.26	6.59
African civet	231	491.49	6.43
Common warthog	193	410.64	5.37
Cow	185	393.62	5.15
Large spotted genet	161	342.55	4.48
Brown hyaena	137	291.49	3.81
Blue wildebeest	131	278.72	3.64
Zebra	129	274.47	3.59
Impala	118	251.06	3.28
Vervet monkey	87	185.11	2.42
Waterbuck	66	140.43	1.84
Eland	58	123.4	1.61
Nyala	52	110.64	1.45
Mongoose**	50	106.38	1.39
Gemsbok	47	100	1.31
Bushpig	45	95.74	1.25
Domestic dog	43	91.49	1.2
Klipspringer	40	85.11	1.11
Common duiker	37	78.72	1.03
Red duiker	31	65.96	0.86
Caracal	30	63.83	0.83
Dassie***	17	36.17	0.47
Black-backed jackal	12	25.53	0.33
Sheep	10	21.28	0.28
Sharpe's grysbok	9	19.15	0.25
Aardvark	8	17.02	0.22
Sable	5	10.64	0.14
Samango monkey	4	8.51	0.11
Bat-eared fox	3	6.38	0.08
Steenbok	1	2.13	0.03

Species	Number of capture events*	RAI	RAI (%)
Blesbok	0	0	0
Goat	0	0	0
Ostrich	0	0	0
Red hartebeest	0	0	0
Small spotted genet	0	0	0

*Capture events were separated by 60-minute intervals (for methods refer to section 5.3.3.2).

**Although mongoose species could be identified at a species level using the camera traps, I grouped all camera trap events of mongoose together because it was not possible to differentiate mongoose species in the scats.

***It was not possible to differentiate between yellow-spotted dassie and rock dassie from the camera trap images so I grouped both dassie species together.

With a Jacobs' index value of 1, small spotted genet, red hartebeest, ostrich, goat, and blesbok are strongly preferred by brown hyaenas (Figure 7.8). Samango monkey and steenbok are also greatly favoured. Other preferred species with a score of 0.6 or higher include common duiker, sheep, dassie, bat-eared fox, bushpig, red duiker, and sable. Cape porcupine is strongly avoided compared to its high relative abundance. Giraffe, large spotted genet, African civet, klipspringer, blue wildebeest, and domestic dog are not highly consumed compared to their relative abundance, suggesting avoidance by brown hyaenas.

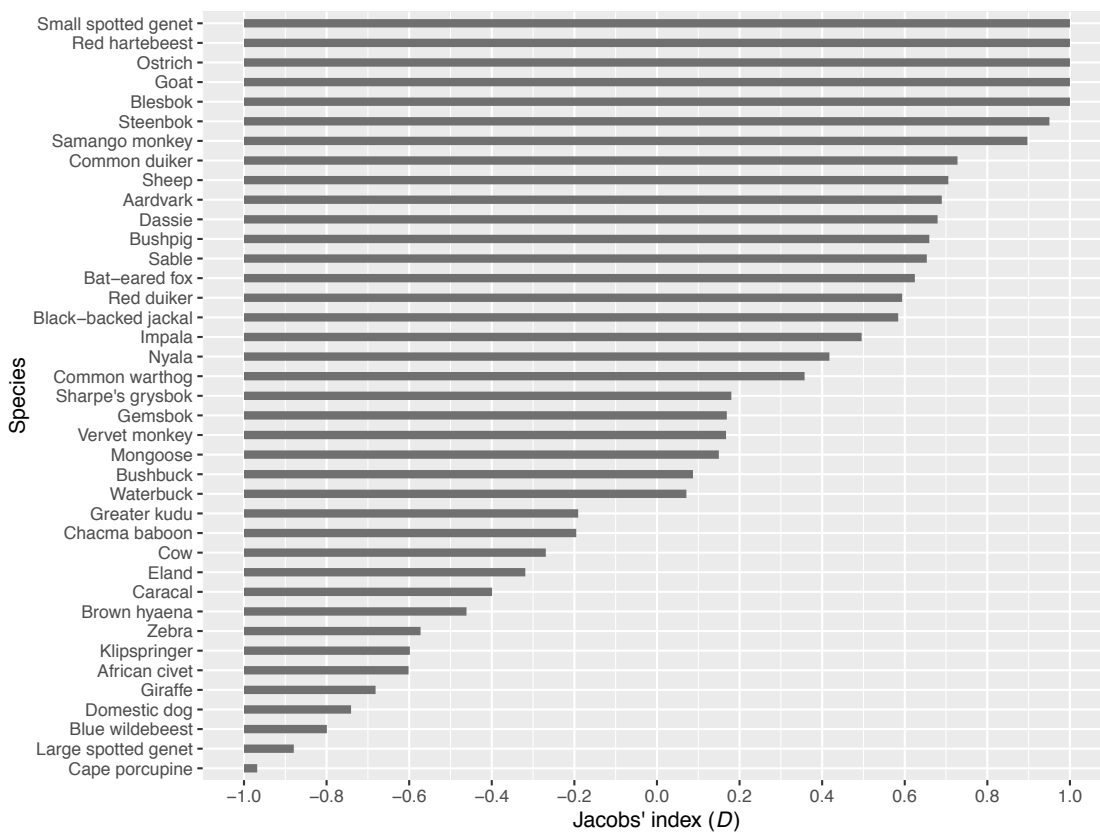


Figure 7.8 Brown hyaena prey preferences in the western Soutpansberg Mountains determined using the Jacobs' index. A score of 1 indicates complete preference and a score of -1 denotes complete avoidance.

The cape porcupine's high RAI value acts as an outlier within the dataset (Table 7.3) and was removed when testing whether there was a significant relationship between the RAI of a species and its corrected occurrence within the scats. A significant effect is detected (linear regression: $F = 13.68$, $DF = 36$, $p = 7.197 \times 10^{-5}$, multiple r -squared = 0.275, gradient = 0.02, intercept = 3.8) (Figure 7.9).

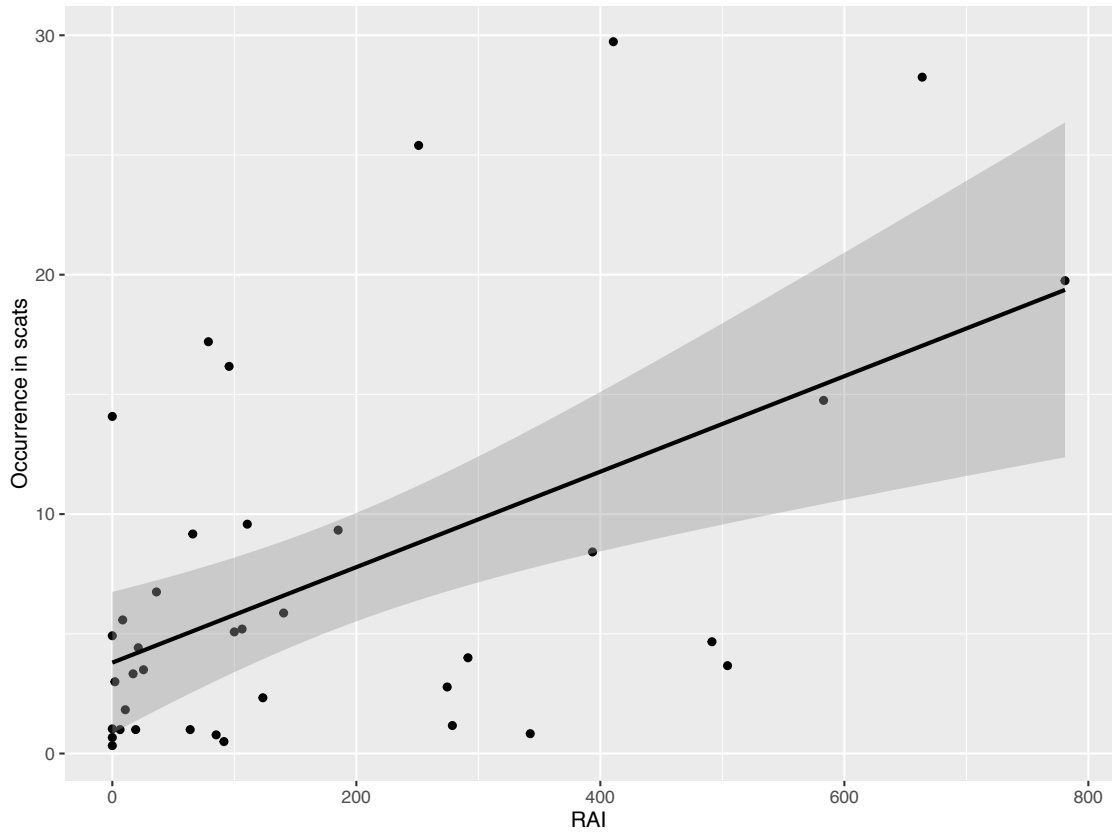


Figure 7.9 Occurrence of species in brown hyaena scats collected in the western Soutpansberg Mountains against species RAI values. Dark grey area is the 95% confidence interval.

7.3.4. Diet composition and commercial hunting prevalence

The most commonly hunted species is impala (39%) (Table 7.4). Common warthog, greater kudu, and blue wildebeest all comprise between 11 and 17% of hunts. The majority of the commercially hunted species in 2014 or 2015 are detected in the brown hyaena diet in the same years. Species that are hunted but are not detected in the brown hyaena diet at all such as mountain reedbuck and buffalo comprise less than 1% of the total hunted animals.

Table 7.4 Species hunted on four commercial hunting farms in or near the Soutpansberg Mountains in 2014 and 2015. Species with no shading were found in the brown hyaena scats in 2014 or 2015. Species with light shading were found in the brown hyaena diet in years aside from 2014 or 2015. Species with dark shading were not detected in any analysed brown hyaena scats.

Hunted species	Total animals hunted in 2014 and 2015	Percentage occurrence (%)
Impala	172	39.00
Common warthog	73	16.55
Greater kudu	49	11.11
Blue wildebeest	49	11.11
Waterbuck	29	6.58
Chacma baboon	16	3.63
Gemsbok	11	2.49
Zebra	8	1.81
Nyala	6	1.36
Blesbok	5	1.13
Giraffe	4	0.91
Eland	4	0.91
Steenbok	3	0.68
Mountain reedbuck	3	0.68
Buffalo	3	0.68
Red hartebeest	2	0.45
Bushbuck	2	0.45
Common duiker	1	0.23
Black-backed jackal	1	0.23

There is no correlation between commercially hunted species occurrence and species occurrence within the brown hyaena diet in 2014 and 2015 combined (Spearman's Rank Correlation: $Rho = 0.244$, $S = 9327.8$, $p = 0.119$). There is no correlation between the level of hunting corrected for abundance and the species occurrence within the brown hyaena diet (Spearman's Rank Correlation: $Rho = -0.207$, $S = 676.1$, $p = 0.458$).

7.3.4.1. Dietary differences between hunting and non-hunting season

Of the analysed scats, 161 were collected during the five months of hunting season annually between 2011 and 2016, and 127 were collected during the seven months of

non-hunting season annually. To account for differences in the frequency of scat collection between hunting seasons and non-hunting seasons, I divided species occurrence in the diet by the number of scats collected in each cumulative set of seasons. There is no significant difference in the rate of species occurrence between hunting and non-hunting season (Wilcoxon signed rank: $V = 576$, $p = 0.902$).

7.3.5. A comparison of leopard diet and brown hyaena diet

Leopard scats collected in the western Soutpansberg Mountains between 2011 and 2015 contained 24 mammal species (Table 7.5). The five most frequently recorded prey species are bushbuck, bushpig, vervet monkey, chacma baboon, and common duiker. Three of these species (bushbuck, chacma baboon, and common duiker) also rank in the top five most commonly found species in the brown hyaena diet.

Table 7.5 Leopard diet in the western Soutpansberg Mountains. Data collated from Fitzgerald (2015) and Sheppard (2016). Data ordered by combined corrected frequency of occurrence.

Species	Corrected occurrences per survey	Source	Combined corrected occurrence	Combined corrected frequency of occurrence (%) (n = 237)
Bushbuck	24.67	Sheppard (2016)	80.83	34.11
	56.17	Fitzgerald (2015)		
Bushpig	7.33	Sheppard (2016)	24	10.13
	16.67	Fitzgerald (2015)		
Vervet monkey	8.5	Sheppard (2016)	19.83	8.37
	11.33	Fitzgerald (2015)		
Chacma baboon	9.5	Fitzgerald (2015)	16.83	7.1
	7.33	Sheppard (2016)		
Common duiker	5.67	Sheppard (2016)	15.67	6.61
	10	Fitzgerald (2015)		
Rock dassie	3.33	Sheppard (2016)	12.17	5.13
	8.83	Fitzgerald (2015)		
Yellow spotted dassie	2.5	Sheppard (2016)	11.5	4.85
	9	Fitzgerald (2015)		
Red duiker	2	Sheppard (2016)	8.83	3.73
	6.83	Fitzgerald (2015)		
Samango monkey	3.5	Sheppard (2016)	7	2.95
	3.5	Fitzgerald (2015)		

Species	Corrected occurrences per survey	Source	Combined corrected occurrence	Combined corrected frequency of occurrence (%) (n = 237)
Common warthog	2.83	Sheppard (2016)	6.33	2.67
	3.5	Fitzgerald (2015)		
Greater kudu	1	Sheppard (2016)	6	2.53
	5	Fitzgerald (2015)		
Klipspringer	5.67	Fitzgerald (2015)	5.67	2.39
Cape porcupine	1	Sheppard (2016)	5.17	2.18
	4.17	Fitzgerald (2015)		
Waterbuck	2	Sheppard (2016)	4	1.69
	2	Fitzgerald (2015)		
Impala	0.5	Sheppard (2016)	3.83	1.62
	3.33	Fitzgerald (2015)		
Rock elephant shrew	1	Sheppard (2016)	2	0.84
	1	Fitzgerald (2015)		
Mountain reedbuck (<i>Redunca fulvorufula</i>)	1.5	Fitzgerald (2015)	1.5	0.63
Four striped mouse	1	Fitzgerald (2015)	1	0.42
Gambian giant rat	0.5	Sheppard (2016)	1	0.42
	0.5	Fitzgerald (2015)		
Grey rhebok (<i>Pelea capreolus</i>)	1	Fitzgerald (2015)	1	0.42
Thick-tailed bushbaby	1	Sheppard (2016)	1	0.42
Namaqua rock mouse (<i>Aethomys namaquensis</i>)	0.5	Fitzgerald (2015)	0.5	0.21
Woodland dormouse (<i>Graphiurus murinus</i>)	0.5	Fitzgerald (2015)	0.5	0.21
Blue wildebeest	0.33	Sheppard (2016)	0.33	0.14

Pooled leopard scat analysis results from Fitzgerald (2015) and Sheppard (2016) were tested for overlap with frequencies of species occurrence in brown hyaena scats. When all brown hyaena scats (n = 288) and all leopard scats (n = 237) were compared, the dietary overlap was 0.66 (Pianka's index), indicating a biologically significant level of overlap. When only brown hyaena scats collected within 10 km of Lajuma were included (n = 202), the dietary overlap increased to 0.74 (Pianka's index).

There is a significant difference between the leopard and brown hyaena diet when the corrected occurrence of species in all brown hyaena scats is compared to the corrected occurrence of species in all leopard scats (Wilcoxon signed rank: V = 867, p = 0.011). No significant difference exists between the corrected occurrence of species in

all brown hyaena scats collected within 10 km of Lajuma and the corrected occurrence of species in the leopard diet (Wilcoxon signed rank: $V = 748.5$, $p = 0.176$).

7.4. Discussion

This study represents the third largest sample of brown hyaena scats analysed after Skinner (1976) who analysed 594 scats and Mills and Mills (1978) who analysed 383 scats. The majority of previous studies examined less than 100 scat samples. To detect all prey species present in a species' diet analysis of at least 59 scats is recommended (Trites and Joy, 2005). For more robust analyses which examine seasonal and spatial differences at least 94 scats are required (Trites and Joy, 2005). As shown by the asymptote in the species accumulation curve, this survey exceeds these recommendations, assuring a sufficient sample size.

The diversity of prey occurrences calculated using the Brillouin index, is more than twice as high as studies which used the Brillouin index to examine brown hyaena dietary diversity elsewhere (van der Merwe *et al.*, 2009; Yarnell *et al.*, 2013). High dietary diversity concurs with the high number of species found in the scats and supports hypothesis 7.2. Forty-seven mammalian species and one avian species were detected. Some plant material was present in scats but this was infrequent compared to drier biomes (Owens and Owens, 1978), suggesting that brown hyaenas fulfil their water requirements elsewhere such as from free-flowing water courses. I found invertebrate exoskeletons in two scats and this can indicate scavenging (van der Merwe *et al.*, 2009). The number of different species found is higher than brown hyaena dietary studies conducted on private farmland elsewhere (Burgener and Gusset, 2003; Maude and Mills, 2005; Ramnanan *et al.*, 2016; Stein *et al.*, 2013). In some cases, this may be because other studies collected a small number of scats over a short period of time and therefore species detection may not have reached asymptote, or because of an inability to distinguish all scat contents to species levels and instead a broad grouping such as small antelope was used. The high content variety is comparable to other studies that analysed large volumes of brown hyaena scats or food remains over extended periods (Mills and Mills, 1978; Owens and Owens,

1978; Yarnell *et al.*, 2013). In addition to methodological differences, it is likely that LUT and habitat diversity within the study area is higher than areas sampled in other studies conducted on farmland. The wide variety of LUTs and habitats within the large study area generate a high level of mammalian biodiversity (Gaigher and Stuart, 2003) (refer to Appendix 6 for a list of species photographed during the occupancy camera trap survey). When combined with the brown hyaena's generalist feeding behaviour, this results in a high diversity of prey species detected within the scats.

In the western Soutpansberg Mountains, recent studies examining leopard scats positively identified 22 mammal species (Fitzgerald, 2015) and 18 mammal species (Sheppard, 2016). This diversity is higher than an earlier study which detected 12 mammal species (Chase Grey, 2011). The greater variation of species found in brown hyaena scats compared to leopard scats may be attributed to the brown hyaena's more generalist and catholic dietary preferences (Burgener and Gusset, 2003; Mills and Mills, 1978; Owens and Owens, 1978).

The majority of faecal samples contain hair from more than one species with two samples including as many as five species. Multiple medium or large sized species were found in scats containing four or five animals. This finding is not uncommon in hyaenid species; as many as seven prey items per scat have been recorded in striped hyaena faeces (Alam and Khan, 2015). High variation per scat is attributed to scavenging and generalist dietary preferences (Alam and Khan, 2015). The high level of species per scat advocates that brown hyaenas conduct regular scavenging behaviour in this area.

The most commonly consumed species match more closely with previous dietary studies conducted on private farmland (especially Burgener and Gusset, 2003; Ramnanan *et al.*, 2016; Stein *et al.*, 2013) than studies conducted within protected areas. Common warthog is the most frequently consumed species in this study and it is the second most common food source on farmland in Namibia (Stein *et al.*, 2013). Bushbuck is the second most commonly consumed species and it is the most commonly consumed species on game and livestock farms in the Waterberg region of Limpopo Province (Ramnanan *et al.*, 2016). Impala is the third most common food

source in this study and also in scat analysis conducted on a game farm in Limpopo Province (Burgener and Gusset, 2003).

Medium and large sized animals comprise the largest part of the brown hyaena diet (78%). Very small animals only account for 3% of the overall feeding occurrences. In studies which have observed successful brown hyaena hunts (which are rare), prey have been restricted to small or very small mammals (Maude, 2005; Mills, 1976). The presence of small or very small species in the brown hyaena diet is less likely to be attributable to scavenging since an apex predator will seldom leave remains from a small meal (Ackerman *et al.*, 1984). This suggests that small and very small mammals within the brown hyaena diet may be the product of successful hunting rather than scavenging.

Carnivore species were detected in 7% of the brown hyaena diet. This supports visual findings at a den site (Figure 3.4) and statements by farmers (Chapter 3). Carnivore species are not uncommon in brown hyaena dietary studies elsewhere. Black-backed jackal and leopard hair occurred in brown hyaena scats on Namibian farmlands (Stein *et al.*, 2013). Along the Namibian coast, brown hyaenas were observed eating black-backed jackals on six occasions (Skinner *et al.*, 1995). Twenty-three per cent of bone accumulations around brown hyaena den sites in Botswana were from carnivores such as black-backed jackals, brown hyaenas, and bat-eared foxes (Maude, 2005). Black-backed jackal and yellow mongoose hair was found in scat samples within the Waterberg region, South Africa (Burgener and Gusset, 2003).

Brown hyaena hair was detected on nine occasions. Brown hyaena hairs found within scats may indicate scavenging, self-grooming, or inter-species predation (Nilsen *et al.*, 2012) with autogrooming and allogrooming being the most likely outcomes (Mills, 1983; Owens and Owens, 1978). In a study of scats in Limpopo Province, brown hyaena was the most common species found (Burgener and Gusset, 2003).

Brown hyaenas consume the majority of species found in the leopard diet; 81.8% of species found by Fitzgerald (2015) and 83.3% of species found by Chase Grey (2011) are present in brown hyaena scats. An overlap of 0.74 (Pianka's index) when

geographic areas are more congruent indicate that it is probable that brown hyaenas in the western Soutpansberg Mountains are scavenging from leopards regularly, especially medium to large sized animals that occur frequently in the leopard diet such as bushbuck (Chase Grey, 2011; Fitzgerald, 2015). These findings are agreement with hypothesis 7.1. A comparison of leopard dietary studies globally show that they prefer to consume prey weighing between 10 and 40 kg with the greatest preference for prey massing 25 kg (Hayward *et al.*, 2006). Species of this size are prevalent in both the leopard and brown hyaena diet. In the Kgalagadi Transfrontier Park, brown hyaenas rarely scavenge from leopards because leopards frequently drag their kills up into trees to reduce competition (Mills and Mills, 2010). Void of the presence of other large carnivores like lions, leopards are not known to hoist kills into trees in the study region, thus enabling greater scavenging possibilities for brown hyaenas. On Namibian farmlands, diets of leopards and brown hyaenas are similar and brown hyaenas scavenged at 76% of 29 monitored leopard kills (Stein *et al.*, 2013). This scenario correlates with accounts of brown hyaenas stealing or scavenging from leopards elsewhere (Mills, 2015; Owens and Owens, 1984; Owens and Owens, 1978).

Dietary examination for three large carnivores (spotted hyaena, African wild dog, and lion) in Cameroon indicate that these species prefer the most abundant prey (Breuer, 2005). Similarly and in support of hypothesis 7.3, a significant relationship was detected between the RAI of a species and its corrected occurrence within the brown hyaena scats. This may correlate with the finding that brown hyaenas are probably scavenging upon leopard kills. Leopard diet in the area is associated with abundance in two species that are very commonly consumed, bushbuck and vervet monkeys (Fitzgerald, 2015). Other species are consumed less or more than expected compared to their availability (Fitzgerald, 2015).

The Jacobs' index shows that brown hyaenas have an absolute preference for small spotted genet, red hartebeest, ostrich, goat, and blesbok with a score of one. These results are somewhat misleading because these species were not photographed during the camera trapping survey. Brown hyaenas may have consumed these animals outside of the camera trapping survey grid yet defecated them within the grid's boundaries. Brown hyaenas travel large distances nightly (Owens and Owens, 1978).

Consequently, feeding sites and defecation sites are not always congruous (Ott *et al.*, 2007). Prey remains in the gut of captive African wild dogs for an average of 79.4 hours (Davies-Mostert *et al.*, 2010). The morphologically similar brown hyaena can move a substantial distance in this amount of time and therefore the location where a scat is collected might not reflect the environment or prey availability where the food was actually consumed. As brown hyaenas often travel greater distances daily and occupy larger home ranges than leopards (Chase Grey, 2011; Martins and Harris, 2013; Stein *et al.*, 2011), discrepancy between the source of the food and the defecation point may also impact the dietary overlap between the two species. Omission of results with an absolute value of one in the Jacobs' index is therefore suggested.

Another factor that may have skewed the accuracy of the Jacobs' index results is the likelihood of a species to be photographed. For example, samango monkeys are largely arboreal (Harvey *et al.*, 1987), thereby reducing the probability of photographing them at ground level. This may give samango monkeys an artificially low RAI, which does not represent their true abundance. This will cause an inflated level of preference.

However, many results indicated in the Jacobs' index as preferred or avoided are likely to offer an accurate representation. The brown hyaena's most avoided species is the cape porcupine. The porcupine's quills make it a dangerous prey item to hunt (Fitzgerald, 2015) or even scavenge from. Other species which rank highly as avoided compared to their availability include giraffe and blue wildebeest. These animals fall outside of the leopard's preferred prey species weight range as described by Hayward *et al.* (2006). Unlike lions which hunt in prides and can tackle very large prey (Hayward and Kerley, 2005), adult giraffe or blue wildebeest are too large for a solitary hunter like a leopard to attack. Considering the dietary dependence between the brown hyaena and the leopard, these species would also be difficult for brown hyaenas to consume unless these animals died naturally or are scavenged as human hunting remains.

Compared to the abundance of cows and domestic dogs, brown hyaenas avoid these species, showing a preference for wild species. I found the opposite trend for sheep and goats, which are consumed more frequently than expected. This may be because

farms with small stock are located outside of the camera trapping grid and, therefore the faeces are deposited within the camera trapping grid's boundaries yet the animals are not photographed. A larger camera trapping area is suggested for future research to resolve this problem.

The brown hyaena's varied and adaptable diet contributes to its success in human-dominated landscapes. Livestock can be a dependable food source for brown hyaenas (Maude and Mills, 2005), spotted hyaenas (Yirga *et al.*, 2013), and striped hyaenas (Alam and Khan, 2015) in agricultural areas. The presence of livestock in hyaenid scats can be an indicator that wild food sources need to be preserved to reduce conflict (Alam and Khan, 2015). In this study, goat, cow, and sheep were found in brown hyaena scats at a low level, confirming hypothesis 7.5. Goat is the most common livestock species and is the eighth most commonly consumed species overall. This finding is not surprising as personal communication with farmers indicates that remains of livestock carcasses are often left in the bush for brown hyaenas and other scavengers to clear. Alternatively, some farmers also stated that brown hyaenas are actively killing their livestock (Chapter 4). There are limitations in making assumptions about how brown hyaenas secure the domestic animals found in their scats. Although no livestock occurred in the leopard diet across locally conducted dietary studies (Chase Grey, 2011; Fitzgerald, 2015; Sheppard, 2016), my observations working for the Primate and Predator Project confirm that leopards do occasionally attack livestock in the area, although this is probably a less frequent occurrence than perceived by farmers. Therefore, brown hyaenas may secure some livestock from leopard remains. The high number of species found per scat, the presence of insects in scats, and reports of farmers leaving discarded carcasses in the bush, suggest (although not conclusively) that scavenging of livestock is a more probable source than hunting.

Although game species are commonly consumed, the majority of these species are not considered high-value game (maximum average price of >10,000 South African Rands per animal, (Pitman *et al.*, 2016b)). No interviewees complained of brown hyaenas killing or having a negative effect on high-value game. High-value game species consumed by brown hyaena include giraffe, klipspringer, sable, and bushbuck. Together three of these species (giraffe, klipspringer, and sable) only account for

2.18% of the dietary occurrences. Contrastingly, bushbuck forms a large part of the diet and is the second most commonly found species. In the western Soutpansberg Mountains, bushbucks are abundant with the third highest RAI level. Therefore, despite the high economic value ascribed to bushbucks, the considerable local natural abundance of the species shapes perceptions of it being commonplace and less valuable. Consequently, the important role that bushbuck plays in the brown hyaena diet is not negatively construed by local people.

Commercial hunting remains are important to scavenger communities worldwide (Mateo-Tomás *et al.*, 2015). Trophy hunting leftovers have a significant effect on spotted hyaena ranging behaviour (Cozzi *et al.*, 2015). Contrastingly and in rejection of hypothesis 7.4, commercial hunting remains do not have a large impact on brown hyaena diet in this area. I found a significant difference between commercially hunted species occurrence and occurrence in the brown hyaena diet. There was no significant difference in brown hyaena diet between hunting and non-hunting season, reinforcing this finding. In areas where commercial hunting properties compose a larger proportion of the local LUTs, this finding might differ. The high density of leopards in the area and the brown hyaena's reliance upon them as a food source may cause a lower than expected level in exploitation of commercial hunting remains. Securing food from leopards may have lower associated risks than moving into areas with higher human activity to access hunting remains.

Aside from the availability of commercial hunting remains, human activity can also offer other scavenging opportunities. Carcasses may become accessible throughout the year from problem animal killings (especially of common warthogs and chacma baboons), non-commercial hunting, culling, injured animals from hunting attempts, and disease spread by farming practices (B. Botha, pers. comm.). Natural disease and drought also present scavenging opportunities. One nearby hunting farm reported the deaths of 16 medium to large game animals due to a drought between January and May 2016 alone with many more deaths predicted. If livestock remains and non-commercially hunted carcasses could also be included in these analyses, a better understanding of how human farming and hunting practices influence brown hyaena diet might be ascertained.

Discrepancies between predator diets and perceived predator diets are common. In Botswana, farmers believe that cheetahs hunt expensive game species like springbok (*Antidorcas marsupialis*), but scat analysis determined that their diet is largely composed of abundant and less commercially valuable species like greater kudu (Boast *et al.*, 2016). Interview data suggests that some farmers believe brown hyaenas target livestock. Domestic animals occur in brown hyaena scats, but at a much lower level than more commonly found wild species, suggesting that the damage brown hyaenas are occasionally perceived to cause is greater than the reality. This is analogous to findings comparing the leopard diet and perceived levels of leopard predation on livestock in the area (Chase Grey, 2011).

One interviewee said that he received reports of brown hyaenas killing lambs, but when he checked, the spoor belonged to domestic dogs. Poachers from a neighbouring community were hunting with dogs and the farmer blamed the losses on brown hyaenas. Sharing the outcomes of this dietary study with local farmers, especially in regards to the evidence pointing to a high frequency of scavenging, may reduce incorrect assumptions of blame and instigate closer assessments when losses occur. Results of this study will be shared with local people and will hopefully be able to act as a conservation tool as suggested by Winterbach *et al.* (2013).

7.4.1. Methodological suggestions

As determined through an analysis of faecal dietary diversity and the Brillouin index, the amount of scats sampled is sufficient to reach asymptote. Based on the point of asymptote, it is suggested that at least 100 brown hyaena scats are sampled to thoroughly comprehend brown hyaena diet at a particular study site. The majority of publications on brown hyaena scat analysis fall short of this target and therefore may not have gained a full picture of dietary scope.

Although some studies rely entirely on cross-sectional analysis and exclude cuticle prints (Boast *et al.*, 2016; Davies-Mostert *et al.*, 2010; Maude and Mills, 2005), I identified occurrences of some rodent species, the lesser bushbaby, and one

occurrence of klipspringer exclusively from the cuticle prints. These species may have been missed from the 20 random hairs selected for cross-sectional analysis because they either occurred infrequently in the scat or they became lost in the wax due to their small size. Therefore, a combination of cross-section and cuticle print analysis is recommended to gain greater confidence in species identification and to detect smaller mammals accurately.

Scat analysis may underestimate the dietary contribution of non-mammalian sources. Through observation, it was determined that in the Kgalagadi Transfrontier Park wild fruits make up 23% of the brown hyaena diet, yet this level of consumption was not detected in scat analysis (Mills, 2015; Mills and Mills, 1978). As this study principally concentrated on the identification of hairs, other sources of food such as insects, birds, or plant materials may be underrepresented. Identification of bone fragments at a species or order level may enable greater insight. Visual observations of habituated individuals would offer truer feeding accuracy. Unfortunately, this approach is not possible in a thick montane environment such as the area this study largely concentrated around, but could potentially be conducted on flatland areas nearby.

7.5. Summary

Two hundred and eighty-eight scats identifiable to a species level were collected between 2011 and 2016. This is a sufficient sample size according to results from the Brillouin index. Multiple species were found per scat (between 1 and 5) with an average of 1.95 species per scat.

I identified 47 mammalian species and one avian species in the brown hyaena diet. The most consumed species is common warthog. Bushbuck, impala, and chacma baboon are also recorded frequently. Animals in the taxonomic order Cetartiodactyla account for 72% of all prey occurrences. Large species weighing between 15 and 50 kg are the most commonly consumed. Domestic animals account for 9.35% of all feeding occurrences.

Overlap between the leopard and brown hyaena diet is high. When brown hyaena scats samples are constrained to the same geographic area as the leopard scats, the overlap increases. It is likely that brown hyaenas scavenge remains from leopards on a regular basis. If the leopard population density in the Soutpansberg Mountains continues to decline as predicted by Williams *et al.* (in review-b), this may be a catalyst for change in the brown hyaena diet and may encourage greater hunting behaviour.

The abundance of prey species is significantly related to the brown hyaena diet suggesting that brown hyaenas consume more abundant prey. Similar findings have been ascertained in the leopard diet locally (Fitzgerald, 2015) and may account for this result.

No relationship was found between the brown hyaena diet and commercial hunting prevalence, suggesting that although scavenging from commercial hunts may supplement the brown hyaena diet, it is not the most important factor. Similarly, no significant difference was found between the brown hyaena diet during hunting season and non-hunting season. Reliance on food sources hunted by leopards may be perceived as less risky than accessing hunting remains.

Although it is impossible to determine with absolute certainty how much of the brown hyaena's food sources are scavenged and how much are hunted, high species variety within scats, wide overall species diversity, the presence of invertebrates, a strong overlap with the leopard diet, and the low prevalence of small mammals suggest that brown hyaenas in and around the Soutpansberg Mountains are chiefly scavengers. Therefore, it is likely that domestic animals found in the brown hyaena diet (goats, cows, sheep, and domestic dog) are scavenged rather than killed by brown hyaenas. This contradicts some accounts by farmers and communities that brown hyaenas frequently kill their livestock. The results of this dietary study will be disseminated back to the community to help improve understanding about the species' ecology, reduce lethal behaviour towards brown hyaenas based on fears of livestock predation rather than evidence, and to illustrate the benefits of scavengers on private land.

Chapter 8: Discussion and conclusions

8.1. Introduction

This thesis investigated relationships between humans and brown hyaenas in and around the Soutpansberg Mountains, Limpopo Province, South Africa. Through an interdisciplinary approach, I determined how brown hyaenas are perceived from various socio-economic perspectives and how these views shape the way people interact with the species. In order to establish how well founded perceptions about brown hyaenas are, I used biological methods to uncover information about brown hyaena density in a montane environment, occupancy of a wider area, dietary composition, and ranging behaviour.

Studies that examine animals using only biological mechanisms may neglect human needs and cultural sensitivities when suggesting practical conservation initiatives (Mascia *et al.*, 2003), and as a result human-wildlife issues behind human-wildlife conflict remain unresolved (Madden and McQuinn, 2014). Conversely, studies that focus entirely on social sciences may be overly human-centric and miss important biological clues which can help explain social interpretations (Udry, 1995). Through an interdisciplinary approach, I applied well-balanced consideration for human and brown hyaena needs to all conservation suggestions.

This chapter summarises, unites, and reviews all research findings (Chapters 3, 4, 5, 6, and 7), reflects upon the interdisciplinary process, and prescribes suggestions for conservation management and future research.

8.2. Summary of research findings through an evaluation of research objectives

Aim 1: Discover how people from different cultural and socio-economic backgrounds living in and around the Soutpansberg Mountains relate to brown hyaenas.

Objective 1: Investigate how perceptions of and attitudes towards brown hyaenas vary between people from different backgrounds and cultures (Chapter 3)

Objective 2: Explore direct and indirect experiences with brown hyaenas (Chapter 3 and Chapter 4).

Results pertaining to objective 1 and objective 2 are presented together as they are strongly interlinked.

Perceptions and experiences of brown hyaenas vary between the three socio-economic groups and even within groups. Private commercial landowners and managers (group A) have the greatest exposure to brown hyaenas. Brown hyaenas are present on most group A interviewees' land and 78% of people in this group have seen a brown hyaena at least once. Many respondents like brown hyaenas and have the most positive outlook towards them. Some group A respondents value them for their ecosystem services or as a draw for tourists. The brown hyaena's secretive nature stimulates perceptions within this group that brown hyaenas are rare and special animals. The positive attitudes held by this group may result from their high overall level of education. Members of this group with lower education levels have more negative attitudes towards brown hyaenas. In addition, positive attitudes are often conditional based on hyaenas displaying 'acceptable' behaviours such as avoiding livestock. If hyaenas violate these conditions, they are perceived as a bother and may become a target for retaliatory actions.

For some group A landowners or managers brown hyaenas pose a threat, either real or perceived, to their livestock, game, and even vegetables. Game farmers are more

accepting of depredation in comparison to livestock farmers. The level of acceptance towards predators and predation is also dependent upon how farmers perceive their own role within nature, primarily as either coexisting with nature or domineering over nature. Some farmers aiming for coexistence with nature view incidents of predation as their fault for not implementing enough precautionary measures whilst other farmers, often with a perspective centred around dominance over nature, perceive depredation as the fault of the predator. In some cases, losses of game or livestock are responded to with targeted persecution. Ten brown hyaenas were reportedly killed as a response to depredation or the risk of depredation in the past five years.

A third of commercial landowners or managers experience predation by brown hyaenas of which, half of them do not consider brown hyaenas to be a problem. This is because the damage induced by hyaenas is minor when compared to the severity of problems caused by more destructive and more 'visible' animals like leopards. Therefore, hatred toward hyaenas is buffered by stronger antipathy towards leopards. This presumably results in lower targeted lethal responses towards hyaenas.

Amongst members of a coloured community (group B) attitudes towards brown hyaenas are mixed. Education levels in this group are intermediate between group A and group C respondents. Most people could accurately identify a hyaena (76.7%) but community members have less exposure to brown hyaenas with a lower percentage of people having seen one than group A respondents. Half of group B respondents have seen a brown hyaena but these occurrences are very rare and often the animal is dead when observed due to a road collision or snaring. Many people are older and do not venture into the mountains anymore, thus reducing their chances of encountering wildlife. Some people are very positive about the species and this coincides with a general appreciation of wildlife and nature within the community, which is mainly founded upon naturalistic and aesthetic factors. However, some interviewees are negative about hyaenas and extremely fearful of them. Livestock is mainly kept as a hobby or as a supplement to a main income. Only a few farmers experience depredation by brown hyaenas but aside from one incident, attacks are very infrequent and the damage is limited. The only hyaena reportedly killed by a group B respondent was found injured in a snare and thus the killing was non-retaliatory.

Members of a small black community (group C) have the least direct interaction with brown hyaenas and have very negative attitudes towards them. Overall, this group has very low levels of formal education. Many group C interviewees have poor predator identification skills and despite being confident in their dislike towards hyaenas, many struggle to accurately identify a brown hyaena. The majority of people are fearful of brown hyaenas. The brown hyaena's secretive nature and nocturnal behaviour is perceived negatively as it reinforces ideas that hyaenas are linked to witchcraft. Most people in the community believe in witchcraft (73%) and consequently have a fearful wariness towards hyaenas despite having almost no direct involvement with the species. It is believed that hyaenas can act as a witch's familiar, provide transport for witches, and witches can transform into hyaenas. Nature is largely viewed from a utilitarian perspective and the brown hyaena is generally perceived as lacking a useful purpose, aside from the use of hyaena parts in traditional medicine. Hyaenas are therefore considered to have little value and are not worthy of preservation. Livestock ownership is minimal and brown hyaenas do not cause depredation.

Across all groups, brown hyaenas are victims of road collisions and snaring, indicating that non-targeted threats which are often overlooked may pose serious threats to the population.

Objective 3: Determine the geographical spaces brown hyaenas are perceived to occupy (Chapter 3 and Chapter 4).

A common theme within the interviews is designated spaces for people and designated spaces for wild animals. Hyaenas and other predators are tolerated until they cross an invisible geographical line or a behavioural boundary. The areas where predators are accepted and the behavioural expectations vary between interviewees. Many ecotourism operators are happy to have predators on their land, even if expensive game is hunted as a result. Some livestock farmers and community members have a zero tolerance attitude towards predators on their land whilst others are accepting of their presence if satisfactory behaviour is demonstrated. Several interviewees stated that there are protected areas such as nature reserves or national parks where predators should live. Expecting hyaenas to adhere to multiple

geographical and behavioural expectations unbeknownst to them bestows anthropomorphic qualities of cognition to the animal and is used to place blame on predators, which justifies negative attitudes and actions. A more clear geographical boundary between human and animal spaces is applied by group B respondents. They believe that wild animals live in the mountains and people live in the flatlands. This group has great respect for the mountains and therefore view themselves as invaders of animals' space when they build homesteads near the base of the mountains.

Aim 2: Discover how historical and current disparities in power between groups affect human-brown hyaena relationships.

Objective 4: Investigate how legacies of colonialism and apartheid affect how people from different cultural groups interact with and perceive wildlife today (Chapter 4).

Power relations infiltrate all aspects of human relationships with brown hyaenas and link to historical control over the land and wildlife from colonial times. Some commercial landowners manage their private properties autonomously like isolated empires. Rituals in biltong and trophy hunting, displays of taxidermy predators, and photographs of hunters posing with shot animals are part of the culture and demonstrate colonial messages of domination and mastery over the wild. For group A respondents, human-hyaena relationships are often a process where control shifts back and forth between people and predators. Predators remove control from farmers through depredation or the threat of depredation. In the process, people lose control over their leisure time, finances, confidence, self-image, mental stability, and land. Control is regained through retaliatory killings and displays of power. Fences are a way of segregating people from animals and other people in an attempt to maintain control. Predators violate this authority by passing through properties and tunneling under fences. Killing animals for the sake of killing asserts masculinity and control, and is part of their culture for some group A interviewees.

Access to nature and ideas of dominance over nature vary starkly between socio-economic groups. This is largely due to disparities in access to land ownership,

education, and wealth, which is partially a legacy of colonialism and apartheid. Hunting by white people is seen as a legal, strong, masculine pastime while hunting by black people is often labeled poaching and is perceived as cowardly and illegal. Many group C respondents are scared of the mountains and the animals residing there, while much of the land in the Soutpansberg Mountains is privately owned by group A respondents and is often used for leisure. These disparities in access to nature and perceptions about interactions with nature reinforce divisions from the apartheid, which separate people into groups with few commonalities occupying different geographic areas. The land reform process and black people entering private land to hunt or for other pursuits are perceived as threats to control over private land in much the same way predators are. Landowners respond to human encroachments in a similar manner to predators with displays of power and attempts to regain control.

Aim 3: Establish the occupancy, population density, ranging behaviour, and dietary preferences of brown hyaenas in mountainous and low-lying environments. Compare the results of the ecological investigation with perspectives presented by people.

Objective 5: Determine the population density of brown hyaenas in the Soutpansberg Mountains (Chapter 5).

In the western Soutpansberg Mountains, brown hyaena density was estimated at 2.56 per 100 km² (confidence interval = 1.14) in 2014 and 3.63 per 100 km² (confidence interval = 1.84) in 2015. These densities are similar to estimations at other study sites across southern Africa. However, recently recorded declines in the leopard population in western Soutpansberg Mountains (Williams *et al.*, in review-b) may trigger changes in the brown hyaena population density because causes of mortality in leopards may also affect brown hyaenas and with less leopards, sources for scavenging may reduce for hyaenas. It is predicted that if a decline in leopards continues brown hyaenas will be affected, not only by altering their diet and potentially triggering increased consumption of domestic animals and hunting remains, but also by bringing them to the forefront of hostilities with farmers. Continued population monitoring is suggested.

Objective 6: *Determine which factors affect brown hyaena occupancy (Chapter 5).*

Occupancy is estimated at 0.7895 (S.D = 0.0649) or ~79% of the 4,974.62 km² area sampled. The majority of factors tested do not have a significant effect on brown hyaena occupancy, illustrating their adaptable nature. The most important factor affecting brown hyaena occupancy is avoidance of high human activity. Brown hyaenas are more likely to be detected on properties where landowners have a positive attitude towards them, suggesting a relationship between knowledge of a species, exposure to a species, and attitude. Hyaena detection is also high on properties where brown hyaenas are killed by landowners. Greater mortality may be linked to higher visibility in these locations. Brown hyaena occupancy is greater on properties with game fences. Although no relationship was detected between occupancy and total prey abundance, a correlation was found between occupancy and the abundance of medium size prey and antelope. This may reflect preferentiality of these species as a food source or higher availability of these species in areas that brown hyaenas occupy more often such as game farms. Where large carnivores are present, brown hyaena occupancy is lower. Hyaenas may be avoiding predators due to competition or there could be higher anthropogenic risks in these areas due to the extreme animosity amongst farmers towards leopards and spotted hyaenas. Habitat type has an effect on hyaena occupancy, with the highest occupancy in areas where a mixture of woodland/grassland is found.

Objective 7: *Determine the home range size of adult brown hyaenas and which land use types they frequent (Chapter 6).*

Geographical positioning system (GPS) collar data was only recovered from two brown hyaenas (50%). One hyaena lives almost exclusively in the Soutpansberg Mountains (AM1) while the other was primarily based on the flatlands (AF3). Humans killed AF3 before the collar finished collecting data, thus providing a truncated data set. AM1 has a home range of 169.79 km² (95% T-LoCoH) and a core area of 68.52 km² (50% T-LoCoH). AF3 has a smaller home range of 95.04 km² (95% T-LoCoH) and a smaller core area of 26.32 km² (50% T-LoCoH). Both hyaenas use game farms preferentially over other land use types. Accordingly, hyaena activity levels are lower on game farms than

on livestock farms, agricultural areas, or land used for tourism. This may be because hyaenas feel safer from anthropogenic risks and because they can access more food sources on game farms. Hyaenas may be moving quicker in more dangerous areas to reduce the amount of time spent there. Brown hyaenas prefer roads to non-road areas, regardless of road substrate.

Objective 8: Determine dietary preferences and the extent of livestock consumption by brown hyaenas (Chapter 7).

Brown hyaenas have a catholic diet in and around the Soutpansberg Mountains. Remains from 47 mammal species and one avian species were found in 288 scats. Plant material, invertebrate remains, and hard plastic were also found in scats. Multiple species were found in scats, ranging from one to five, with 1.95 species per scat on average. The five most commonly consumed species are common warthog, bushbuck, impala, chacma baboon, and common duiker. Seventy-two per cent of all prey occurrences are from the order Cetartiodactyla. Medium to large sized animals are consumed most frequently. Domestic animals contribute to 9.35% of all dietary occurrences. Brown hyaenas seldom consume high-value game species aside from bushbuck, which are regionally abundant.

Brown hyaena consume species in proportion to their abundance. Commercial hunting remains may be scavenged by brown hyaenas, but no correlation was found between occurrence of species in the brown hyaena diet and the occurrence of hunted species. In addition, no significant difference was detected between brown hyaena diet in hunting and non-hunting season. This may be because of restrictions in the sampling area or because hyaenas prefer to scavenge from leopards over hunting remains because anthropogenic risks are lower. Brown hyaena diet has a high degree of overlap with leopard diet and no significant difference was found between the occurrence of species in leopard and brown hyaena diet sampled within the same geographic region. Dietary overlap between leopards and brown hyaenas is estimated at 0.74 (Pianka's index).

The presence of invertebrates in scats, low consumption of small or very small mammals, and high overlap with the leopard diet suggest that the majority of feeding occurrences are probably from scavenging. Although some interviewees report livestock depredation by brown hyaenas, the results of the scat analysis suggest that brown hyaenas infrequently consume domestic animals and when consumed, livestock is probably scavenged rather than hunted.

Aim 4: Make suggestions for improving human-brown hyaena relationships and conserving carnivores.

Objective 9: Combine social and biological learning to design conservation strategies, which are shaped around the diversity of groups present in the area (Chapter 8).

Refer to section 8.4.

8.3. Broader contributions of the research

In this thesis I addressed the gaps in the ecological and social knowledge pertaining to brown hyaenas and their relationships with humans at my study site. Mounting evidence suggests that non-protected areas provide vital habitats for brown hyaenas and are essential for the conservation of the species (Kent and Hill, 2013; Lindsey *et al.*, 2013b; Stein *et al.*, 2013). Regardless, much recent research on brown hyaenas is situated on protected land (e.g. Welch and Parker, 2016; Welch *et al.*, 2016; Yarnell *et al.*, 2014). This study explores human-brown hyaena relations in a large non-protected area which hosts a myriad of land use types, thus providing much needed information on brown hyaena ecology and their relations with humans on private land. Additionally, brown hyaenas are understudied in montane areas and this was the first in-depth investigation of the species and their relationships with people in such an environment. More information regarding brown hyaena density and factors affecting occupancy were highlighted as research priorities in the South African national red list assessment for the species (Yarnell *et al.*, in press). This thesis has made a valuable

contribution towards filling this gap. Threats facing brown hyaenas, especially those with anthropogenic origins, are poorly understood. This study established the threats facing brown hyaenas in and around the Soutpansberg Mountains and uncovered new information on the detrimental impacts of snaring and road collisions on the species.

The majority of research on brown hyaenas is site-specific. Unlike other large carnivores in southern Africa, no academic work thus far has compiled published and unpublished data from across multiple study sites or seasons to compare broad trends in particular aspects of brown hyaena ecology or conservation. This has resulted in a patchy comprehension of the species. This thesis has great potential to contribute towards understanding brown hyaenas across their entire range in a cohesive fashion if an integrated multi-author approach is applied. For example, Chapter 6's results on brown hyaena ranging are hindered by a small sample size of collared individuals. However, if these data are united with records from brown hyaena studies conducted elsewhere within southern Africa, similar to how Pitman *et al.* (2016a) combined collar data from multiple sites to explore fine scale leopard resource use, the wider and more applied potential of my data may be realised.

My findings are significant for brown hyaena conservation on a localised and species-specific scale but when synthesized into a broader perspective that includes the entire large carnivore guild, the results gain a wider and more malleable level of importance. Large carnivores are in decline worldwide (Ripple *et al.*, 2016), often as a result of targeted or non-targeted anthropogenic factors (Frank *et al.*, 2005; Sillero-Zubiri and Laurenson, 2001). This thesis can be considered as a case study with brown hyaenas acting as a focal species for the large carnivore guild. This is especially relevant in its interdisciplinary context. An interdisciplinary framework is key to understanding and addressing human-wildlife conflict and planning conservation initiatives (Bennett *et al.*, 2016; Clark *et al.*, 2001; Madden and McQuinn, 2014).

I applied the interdisciplinary findings of this thesis to surrogate species concepts relevant to the entire large carnivore guild through a case study approach (Appendix 7) (Williams *et al.*, in review-a). Leopards provide brown hyaenas with scavenging opportunities and protection from anthropogenic risks and therefore function as a

socioecological keystone species. This represents the first attempt to apply the surrogate species concept within a social framework to assess how human culture can be exploited to benefit wildlife conservation. These results suggest employing a holistic multi-species approach that protects large carnivore guilds rather than a single species approach when planning large carnivore conservation. Extending the surrogate species concept and integrating this within a socioecological framework provides conservationists with a more holistic approach to biodiversity conservation (Williams *et al.*, in review-a).

The importance of mountains as a refuge for brown hyaenas can also apply to other carnivores. An animal's use of space is affected by a number of factors; some of which are correlated with topographical variation. The abundance and distribution of food resources, water sources, the density of competitor species, and human disturbance levels often differ altitudinally (Kohler *et al.*, 2010; Messerli and Winiger, 1992; Viviroli and Weingartner, 2004). Direct human impact is frequently lower in mountainous areas due to inaccessibility and unsuitability for farming (Swanepoel *et al.*, 2013), although the impacts of climate change are higher (Kohler *et al.*, 2010; López-Moreno *et al.*, 2008), therefore mountains can act as immediate wildlife refuges (Chase Grey *et al.*, 2013; Gavashelishvili and Lukarevskiy, 2008). Mountains and their surrounding areas should therefore be preserved, not only for brown hyaenas in the Soutpansberg, but also for the conservation of the entire large carnivore guild.

Human-animal relations, either with wild or domestic animals, frequently examine human values, actions, and personhood (Hurn, 2012). Animals are used as tools to reflect upon humanity (Mullin, 1999). My research expanded upon this theoretical concept, especially in regards to how shifting and unequal power relations within a postcolonial environment are revealed in people's relationships with predators. My exploration of postcolonialism in relation to carnivore conservation is novel and makes an important contribution to the emerging theme of how historical legacies affect present day human-animal relationships (e.g. Rust and Taylor, 2016; Rust *et al.*, 2016). I investigated power relations through dual perspectives – powerful predators and powerful people – and ascertained their effects upon human-animal relationships. The themes identified and the repercussions of periods of inequality, especially from

colonisation, are globally applicable and should be acknowledged when planning conservation strategies. Through this approach, underlying human-human issues that may be fueling human-wildlife conflict can be properly understood and addressed.

This thesis is unique in the field of conservation because it considers human-wildlife relations rather than focusing exclusively on human-wildlife conflict. I examined both positive and negative conceptions of brown hyaenas to gain a more holistic understanding of this complex relationship. Relationships with animals are extremely complicated and vary geographically, temporally, between cultures, and even between individuals (Arluke and Sanders, 1996; Lawrence, 2003). By employing a combination of ethnographic methods, I observed extreme variation in participants' relationships with animals between socioeconomic groups and within a relatively small geographical space, thus illustrating the intricacy of human-brown hyaena relationships in and around the Soutpansberg Mountains. This is the first examination of the complexities behind how humans relate to brown hyaenas and the first application of these concepts to the large predator guild, thus making it an important ethnographic work for this particular species and predators in general.

I was able to ascertain how power structures between groups of humans or even between imagined and real versions of one's self affect most aspects of how members of group A interact with wildlife. A similar depth of understanding regarding the human issues behind relationships with predators was not achieved with group B and group C participants. I developed a stronger 'insider' position with group A participants than with respondents from group B and group C. This was partially due to some cultural and linguistic commonalities and partly because the demands of interdisciplinary research did not allow me to spend the time required to fully immerse myself in group B and C's communities. I suggest that investigations of human-animal relationships within interdisciplinary research combine multiple ethnographic methods to aid the in-depth understanding required but that researchers working within a limited time frame cannot expect to achieve this level of insight across a diverse spectrum of people.

In summary, this thesis contributed to the knowledge about brown hyaenas and their relationships with people in an area void of information pertaining to this elusive and understudied species. Equally importantly, these findings have significant implications on broad scale both in an applied and theoretical context.

8.4. Management recommendations

Socio-economic groups have varying values, attitudes towards hyaenas, and experiences of hyaenas (Chapter 3), therefore conservation actions should be tailored to locally specific situations to create effective and nuanced strategies. Hereafter, I present a suite of broad suggestions for the conservation management of brown hyaenas, which should be adjusted in relation to the target audience and geographic area prior to implementation.

Entrust conservation to all people

Appreciation of, access to, and participation in nature are polarised and class-related in South Africa. Although the majority of South Africans are black, this group only represented 8.8% of visitors to South African parks in 2010/2011 (Butler and Richardson, 2015). Factors contributing to wildlife park visitation rates between whites and non-whites included education, income, transport, lack of knowledge, and household size (Butler and Richardson, 2015; Lindberg *et al.*, 2003). Even after controlling for these socio-economic factors, non-whites were less likely to visit. Many non-whites indicate that parks are seen as ‘white areas’ because of the historical context of restricted access and current images such as in advertisements (Butler and Richardson, 2015; Lindberg *et al.*, 2003). Under apartheid, black people were restricted from entering Kruger National Park (Magome and Murombedzi, 2003). Kruger National Park was named after the Afrikaans leader, Paul Kruger, and symbolises Boer nationalism and voortrekker mythology (Adams, 2003; Beinart and Coates, 1995). Even the name is exclusionary, therefore it is understandable why black people may feel that Kruger National Park is not space they belong in and why these feelings may extend to other wild spaces (Adams, 2003; Carruthers, 1997).

When conducting my interviews, many group B and group C respondents were surprised that I lived in the mountains. They asked in astonishment if I was afraid of the leopards and hyaenas. Many of these people have little exposure to nature and see wild places as inhospitable and separate from them. As a result, concepts of conservation are extremely alien to them. Conservation of wildlife is not perceived as something that should involve or affect them.

Conservation today is still mainly designed and driven by European influences with few African-based initiatives (Adams and McShane, 1996). Much of the funding for conservation is secured by high paying western tourists who 'volunteer' their time and money towards helping Africa's wildlife which further westernises and excludes Africans (Cousins *et al.*, 2009). The paradigm of separating black Africans from wildlife continues and in some ways symbolically mirrors the forceful removals of native people from protected land under colonialism and apartheid.

However, it has been proven that conservation is best achieved when communities are involved, given rights to manage and use wildlife on their land, and receive economic or community benefits from wildlife (Emerton, 2001). In addition, the different cultural meanings behind resources should be acknowledged in conservation initiatives and this can only be achieved through community inclusion (Infield, 2001).

I suggest that efforts are made in northern Limpopo Province to include more community members in nature and conservation. Firstly, more exposure to nature at a young age is suggested. Visits by school children to wild places can make a lasting impression on attitudes and access to nature as adults (Thompson *et al.*, 2008). Environmental education, especially when conducted over a longer time period through residential programmes, increases knowledge and improves learners' attitudes towards the environment (Bogner, 1998; Dettmann-Easler and Pease, 1999). Teaching sessions can improve learners' environmental behaviours and influence their parents to follow suit, with long-lasting effects (Boudet *et al.*, 2016). Some local initiatives are already delivering environmental education to schoolchildren. However, due to funding and staffing constraints, the number of schools involved with these programmes is small in comparison to the entire region's school system, and actual

teaching time from environmental educators is limited and often occurs on an ad hoc basis. To overcome these barriers, I recommend greater governmental and non-governmental funding to facilitate school visits to wild places and increased investment in organisations that can deliver environmental education. I also suggest that the government encourages more schools to join the Wildlife and Environment Society of South Africa Eco-Schools programme and provides increased financial support to this programme because it has the unique approach of transforming normal teaching staff into environmental educators and integrating environmentalism holistically into all aspects of school life.

Greater investment in ecotourism ventures is also recommended in northern Limpopo Province to help bridge the gap between local people and nature, and to add value to animals like brown hyaenas which are perceived by black communities to have little utilitarian purpose and are therefore considered undeserving of conservation efforts. When ecotourism is conducted in cooperation with local communities who receive a fair share of benefits, it can be a very successful conservation tool, especially for large carnivores, because it gives animals a tangible economic value and therefore promotes long-term preservation (Sillero-Zubiri and Laurenson, 2001). Careful development of ecotourism in association with communities can empower local people while simultaneously exposing tourists to culture and wildlife, thus improving marketing potential (Herbig and O'Hara, 1997; Reimer and Walter, 2013; Scheyvens, 1999). If indigenous knowledge systems are incorporated into tourism and conservation, it serves a triple purpose of preserving local culture, creating income, and enriching biological understanding (Butler and Menzies, 2007; Gadgil *et al.*, 1993). When combined with more vigorous law enforcement, alternative livelihood opportunities may reduce illegal practices such as poaching and snaring (Lindsey *et al.*, 2013a).

Reduce snaring

Although brown hyaenas are vulnerable to targeted persecution by humans, non-selective methods pose a bigger threat in the study area. As a facultative scavenger, brown hyaenas may be especially vulnerable to indiscriminate threats, especially at

bait stations which may be laced with poison or surrounded by snares intended for other target animals (Knopff *et al.*, 2010).

During the occupancy camera trapping survey and the 2015 SECR camera trapping survey, photographs were taken of brown hyaenas with snares or snare-related injuries (Figure 8.1). While conducting fieldwork, I found snares or carcasses of animals killed in snares on multiple occasions. I found a snare several metres away from where I recovered AF3's collar, for example. The three-legged brown hyaena (pictured in Figure 8.1b) mostly likely lost his limb in a snare. Self-tightening snares are often responsible for amputated limbs through necrosis or the animal gnawing off their own limb (García-Perea, 2000; Obanda *et al.*, 2008; Waller and Reynolds, 2001). Animals that are able to break free from anchors often bring the taut and unreleasable snare with them, which cuts deep into their skin. These abrasions are prone to become infected or septic, or the snare may cause internal injuries, resulting in a prolonged and painful death (Rochlitz *et al.*, 2010). Alternatively, snares can inhibit movement thus reducing hunting or scavenging success and resulting in starvation (A. Tordiffe, pers. comm.).

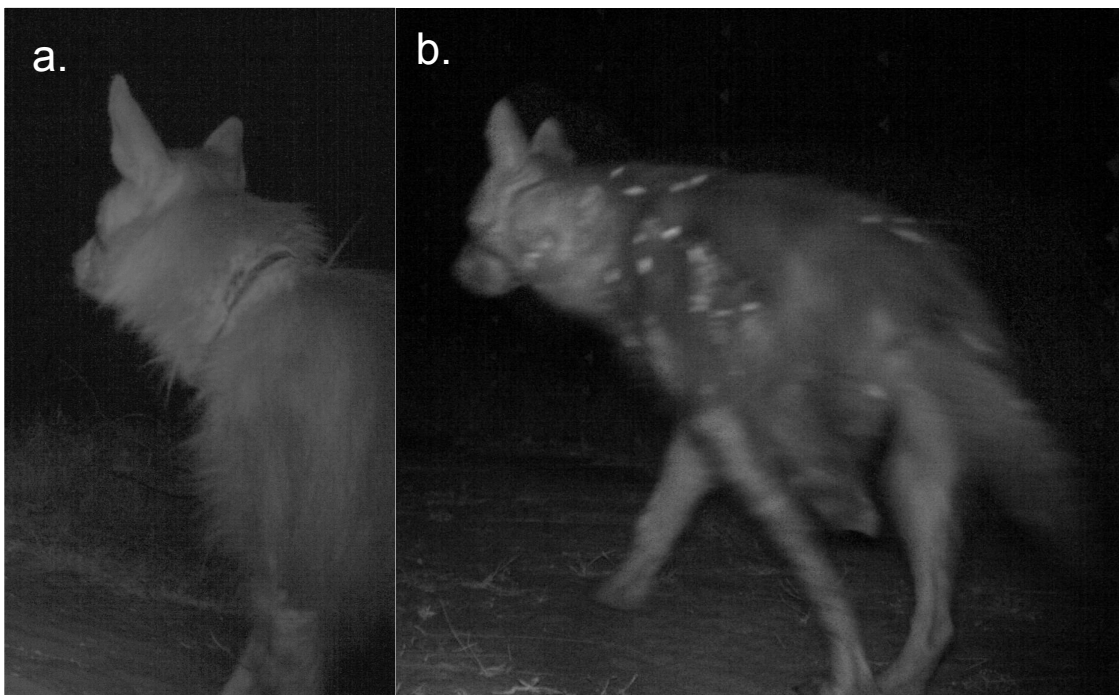


Figure 8.1 The consequences of snaring on brown hyaenas, as recorded during the occupancy camera trap survey conducted in and around the Soutpansberg Mountains. a. A brown hyaena with a snare around his neck. b. A three-legged brown hyaena.

Visible injuries from snaring on live animals are likely to be the tip of the iceberg compared to the number of animals killed by snares at anchor sites. Little research has been conducted on the impact of snaring in large tracts of multi-use private land but based on personal observations and research conducted in protected areas (Becker *et al.*, 2013; Tumisiime *et al.*, 2010; Wato *et al.*, 2006), the impact of snaring on wildlife in and around the Soutpansberg Mountains appears to be astronomical. More research into the causes and effects of snaring is urgently needed (Lindsey *et al.*, 2013a). The Endangered Wildlife Trust is launching a national programme to compile records of snaring instances and to study trends. Landowners and environmental organisations in and around the study site are encouraged to contribute information to this campaign. In addition, a similar initiative is necessary at a more localised level to properly understand and consider area specific factors influencing snaring when responding to the problem.

Although snaring is illegal, it is a common practice in the region. Law enforcement seems lax around tackling poaching and snaring. It is recommended that combatting snaring is prioritised by the police and responded to as a serious crime. At the moment private properties and communities conduct anti-poaching independently with varying levels of success based on their effort, knowledge, support, and financial means (Lindsey *et al.*, 2013a). A united approach with proper law enforcement is required to truly reverse trends.

However, even with more knowledge and greater police involvement, the underlying causes behind snaring are extremely difficult to reverse, especially in a short time period (Lindsey *et al.*, 2013a). The likelihood of snaring is associated with socio-economic factors such as low levels of formal education, economic hardship, food insecurity, unemployment, and household sizes (Lewis and Phiri, 1998; Lindsey *et al.*, 2013a; Tumisiime *et al.*, 2010). These deep socio-economic issues, which are partial remnants from apartheid and colonialism times, require dynamic strategies and investment to counter. Ecotourism and other alternative livelihood opportunities may be one possible angle towards achieving this.

Improve road safety

Roads pose a non-targeted anthropogenic threat to brown hyaenas. Considering the high proportion of time that collared hyaena AF3 spent crossing fast-moving tar roads and the preference for moving on roads over non-road areas in both collared hyaenas, it is not surprising that members in all three interviewee groups experienced instances of road mortality in brown hyaenas.

Road crossing hotspots should be identified and active species-specific signage should be erected at these points to alert motorists. Solar powered flashing amber lights on the signs, which activate at night, are recommended as this is the time when hyaenas are most vulnerable (Sullivan *et al.*, 2004). In addition, wildlife underpasses with large diameters and extended banks are recommended at hotspots (Foster and Humphrey, 1995; Glista *et al.*, 2009).

Change perceptions of brown hyaenas as livestock killers

Livestock does not comprise a large part of the brown hyaena diet at this study site, and in alignment with other academic studies (Maude and Mills, 2005; Mills, 1990; Owens and Owens, 1978; Stein *et al.*, 2013), all evidence indicates that scavenging is prevalent over hunting in food acquisition. Nevertheless, there are still many farmers who believe that brown hyaenas are a threat to their livestock and will kill them when they enter their farms as a preventative precaution or a reactionary measure after finding a livestock carcass. This largely non-scientifically supported view of brown hyaenas as a threat to livestock is maintained in some popular grey literature. The July 12, 2013 issue of the South African farmers' magazine, *Landbou Weekblad* (Farmer's Weekly), depicted sinister looking brown hyaenas on the cover (Figure 8.2) and featured an article entitled "Strandjutte: Die nuwe probleemdiër?" ("Brown hyaenas: The new problem animal?").



Figure 8.2 The cover of Landbou Weekblad magazine, July 12, 2013.

Retaliatory killings of carnivores such as jaguars can be predicted not only from the threats they pose to livestock but also from fears, personal motivations, and other barriers such as low education or political unrest (Marchini and Macdonald, 2012). Replacing unjustified fears and low education with a more accurate understanding of brown hyenas is essential to mitigate retaliatory killings and promote conservation. Negative perceptions of brown hyenas as livestock killers should be replaced with biologically accurate facts about brown hyenas as providing ecosystem services and as primarily scavengers. This will hopefully stop farmers from jumping to immediate conclusions and misassigning culpability when hyena tracks are found near a carcass. The results of dietary studies should be made accessible to the public through appropriate sources such as local newspapers and commonly read magazines like Landbou Weekblad.

It is important to note that scientific evidence does not deny that brown hyaenas hunt livestock (Skinner, 1976; Van As, 2012). It is likely that some of the reports of brown hyaena depredation by interviewees in this study are correctly attributed. However, stock hunting by brown hyaena are often rare incidents that involve lone individuals rather than whole clans (Skinner and Chimimba, 2005; Skinner, 1976). Translocation of problem brown hyaenas has been an effective strategy to solve this problem in Namibia (Weise *et al.*, 2015). Within the study area, government officials no longer perform translocations of problem predators because of previous low success rates (A. McMurtie, pers. comm.). Therefore, non-lethal conflict mitigation approaches such as kraaling livestock in bomas at night or using livestock-guarding dogs are recommended to farmers who have confirmed problems with brown hyaenas or other predators. These approaches can be highly effective (Ogada *et al.*, 2003). Livestock-guarding dogs are almost 100% effective in reducing stock loss if correctly implemented (Leijenaar *et al.*, 2015). Unfortunately, many farmers indicated in their interviews that they feel unsupported or unconfident in tackling conflict with predators. The Primate and Predator Project (PPP) appointed a Community Engagement Officer in 2015 to provide this support and administer training about sustainable methods to coexist with predators. Despite the challenges of sourcing continued funding for this post, it is recommended that all efforts to do so be made because of the extreme value the postholder offers the community and wildlife. It is recommended that similar support is made available in other areas with vulnerable predator populations.

Education programmes targeted at particular groups, increased support from spokespeople within these groups, an integration of human and ecological concerns, and species-specific education can be used to improve perceptions of carnivores and reduce fear which is often the key factor leading to negative views (Kellert *et al.*, 1996; Lagendijk and Gusset, 2008). It is suggested that through education and positive publicity, the image of brown hyaenas as a hindrance to farmers is replaced with an appreciation of their value to farmers for their ecosystem services. Scavengers provide pivotal regulating (disposal of carcasses) and supporting (nutrient cycling) services within the ecosystem (Beasley *et al.*, 2015; DeVault *et al.*, 2003). Through these services, disease transmission is curtailed (Beasley *et al.*, 2015). Ćirović *et al.* (2016) established that in Serbia golden jackals clear over 3,700 t of animal waste and 13.2

million crop pest rodents annually. These services were estimated as having a monetary value of over 0.5 million Euros a year (Ćirović *et al.*, 2016). If a similar financial value could be placed upon the role brown hyaenas play on private land, this could create an environment where brown hyaenas are welcome on farms and in communities, rather than ‘trespassing’.

Enable predator movements both mentally and physically

Brown hyaenas need large home ranges (Chapter 6) to exploit a wide variety of resources. Breaking down mental barriers pertaining to where brown hyaenas belong and how they should act is essential to create large enough spaces for hyaenas to safely move through. This can be achieved by replacing negative ill-informed perceptions with positive ones that comprehend the value of living with predators.

Landscape fragmentation has a negative effect on some large predators in South Africa such as leopards (Swanepoel *et al.*, 2013). Fencing private areas can affect wildlife movements, prey selection, hunting, inbreeding, overstocking, and increase mortality (Beck, 2010; Davies-Mostert *et al.*, 2013).

Physical barriers challenge predators’ movements, especially on private heavily fenced land (Beck, 2010; Davies-Mostert *et al.*, 2013). Although brown hyaenas often navigate through game fences, as seen in other studies (Kesch *et al.*, 2013; Richmond-Coggan, 2014; Wiseman Jones, 2014) and the collaring data from this study, movement is challenged when holes under fences dug by animals are closed up by farm staff causing hyaenas to seek new holes. Neighbouring farmers who are both more amenable to the presence of predators install deliberate and well-constructed passageways under game fences to allow smaller animals to transverse but keep larger game and livestock enclosed (Figure 8.3). Passageways such as these protect the fence line from unsolicited digging of holes (Kesch *et al.*, 2013) and provide a safe area away from electric fencing for animals to pass. It is recommended that more farms install such conduits. Introducing corridors between private land can help to protect the small areas of potentially suitable habitats remaining for predators like leopards (Swanepoel *et al.*, 2013). Also, it is believed that discussions between landowners

about creating passageways can start to break down island mentalities towards the landscape and instill greater cooperation towards accepting predators on private land.



Figure 8.3 A leopard uses an inbuilt passageway between game farms in northern Limpopo Province.

Consider the role of witchcraft in conservation

Of all animals, hyaenas are the most strongly associated with witchcraft at my study site. These associations with witchcraft mean that hyaenas are not safe near black communities, where little sympathy is extended to the species out of fear. Although in my study black community members are the least likely group to come into contact with hyaenas and therefore pose the smallest targeted physical threat to hyaenas, negative perceptions will continue to perpetuate through communicative memory and cultural memory (Assmann and Czaplicka, 1995) unless there is intervention. Fear will prevent younger generations within these communities from connecting with nature and therefore perpetuate a cycle of disengagement with nature. This may prevent them from seeking job opportunities in wildlife tourism and prolong apartheid-like divisions in access to nature. It will also mean that important messages about the inadvertent consequences of snaring will fall on deaf ears.

Intervention strategies and greater information on a species' population status are urgently required for many animals classified as endangered as a result of cultural belief systems. For example, pangolins are declining rapidly across their range due to a demand for body parts in traditional medicine (International Union for Conservation of Nature, 2013). It is suggested that conservation efforts include educating traditional healers and the general public on how unsustainable pangolin harvesting harms the species and biodiversity, and the impact this loss will have upon local community cultural belief systems (Boakye *et al.*, 2015; Soewu and Adekanola, 2011). I suggest that near threatened and threatened species that are adversely affected either directly or inadvertently by cultural beliefs such as brown hyaenas in northern Limpopo Province also require carefully constructed conservation strategies to prevent them from reaching a critically endangered state. Strategies to replace fearful and largely unfounded views of wolves in Scandinavia with more realistic and positive associations emphasise the importance of allowing people time to readjust to new perceptions of wolves (Linnell *et al.*, 2003). This realistic expectation is recommended when disassociating hyaenas from beliefs about witchcraft. It is suggested that education about hyaenas aimed at youth is a key part of the process. In 2014, I wrote and illustrated a children's book about brown hyaenas, which was distributed to teachers at 11 schools in four local languages. The book aims to oust negative stereotypes about brown hyaenas and touches upon changing associations with witchcraft. Environmental education through stories and teaching in school is important to give children a different perspective from the stories they hear at home about witchcraft.

Some postcolonial environmental interventions and education programmes perpetuate colonial discourses, orientalist ideologies, and domination (Crowe and Shryer, 1995; Kideghesho, 2009). Attempts by outsiders to dispel beliefs associated with witchcraft may be perceived to imply that concepts about witchcraft are infantile, archaic, and associated exclusively with poor and uneducated people. Stereotypes such as these are a far cry from the reality of witchcraft in Africa. Members of society who span a spectrum of rural and urban locales, education levels, and access to wealth hold beliefs in witchcraft (Apter; Bastian, 1993). Although beliefs in witchcraft in Africa predate colonialism, colonisation and modernisation considerably redefined experiences and understandings of witchcraft, illustrating its intricate and developing

nature (Apter, 1993; Auslander, 1993; Geschiere, 1997; Niehaus *et al.*, 2001; Schmoll, 1993). Therefore, cultural sensitivity is required when addressing beliefs pertaining to witchcraft, as they represent history and belief structures (Ashforth, 1996; Cumes, 2004). Outsiders, especially from western backgrounds, may fail to fully grasp the dynamism and modern applications of witchcraft and cause offense if the concept's secretive and sensitive characteristics are not respectfully acknowledged (Geschiere, 1997, p. 2). Thus, it is recommended that local community members, especially teachers, church officials, and government officials, lead education efforts that focus exclusively on the animals in need of protection and avoid making wider comment about personal beliefs. Conservation organisations may need to work with local people to ensure that educators have the correct knowledge and tools to deliver information on the ground and to guarantee local perspectives and priorities are integrated in the message.

Preserve the leopard population

Dietary results of this study show a strong overlap between the brown hyaena diet and the leopard diet. Trophic downgrading and specifically the loss of leopards, the apex predator within the study site, will probably have dramatic consequences for the brown hyaena population (Beasley *et al.*, 2015). It is therefore suggested that in order to protect brown hyaenas, conservation measures should be put in place to preserve leopards. The leopard population is in serious decline both at the study site (Williams *et al.*, in review-b) and globally (Jacobson *et al.*, 2016).

Leopard decline is also the result of non-selective methods like snaring (Williams *et al.*, in review-b), therefore taking measures to reverse snaring and poaching would help brown hyaenas two fold – directly by reducing their vulnerability to these threats and indirectly by ensuring the leopard population does not decline. Leopards face greater targeted persecution in response to livestock and expensive game losses than brown hyaenas. Lethal control measures to protect livestock are more costly and less effective than non-lethal approaches (McManus *et al.*, 2015; Treves *et al.*, 2016). It is suggested that farmers adopt sustainable non-lethal approaches to protect their

animals from leopard depredation such as livestock-guarding dogs and kraaling of livestock at night so farming can succeed alongside predators.

8.5. Further research

A sample of only two GPS collared brown hyaenas is not sufficient to make robust assumptions about spatial usage and habitat requirements for the species. The comparison between montane-dwelling and flatland-dwelling hyaenas is somewhat speculative considering that only one hyaena occupies each test area. The results of Chapter 6 could provide a pilot study for further ranging research on brown hyaenas based in mountains and in flatlands. A study focused on several hyaenas occupying both areas could ascertain with statistical significance whether home ranges differ in size. If more hyaenas are initially collared, anthropogenic mortality would hopefully have a smaller impact on the amount of GPS points collected. A small sample size compromised some of the research questions I would have liked to answer. With more data, range size and movement patterns could be investigated between seasons. It would be especially interesting to ascertain if movement changes during hunting and non-hunting seasons, possibly in response to more reliable availability of food in hunting season. The locations of vulture restaurants could be mapped and the frequency of visits to these spots could be analysed year round.

The importance of vulture restaurants could be explored further with dietary analysis, resulting in a deeper understanding of the complexities in the human-brown hyaena relationship. Although spending time near humans is dangerous for brown hyaenas, the benefits of a ready food source may outweigh the threats. I compared the brown hyaena diet to the number of animals hunted or injured during hunting season on four farms within the scat collection area. A more accurate approach would be to monitor the precise amount of animal remains deposited at vulture restaurants and compare this to dietary composition.

Following Valiex *et al.* (2012), livestock posts could be mapped and collar data could be used to determine if visits to kraals occur. Although the results of the dietary

analysis suggest that brown hyaenas ascertain the majority of their food from scavenging, these results are not 100% conclusive. Correlating GPS points with live cattle locations would provide further insight. More evidence about whether brown hyaenas pose a predation threat to livestock is essential for changing perceptions and creating management plans.

I was only able to conduct spatially explicit capture recapture (SECR) density estimates in the Soutpansberg Mountains due to geographically specific access to resources provided through Panthera. For a greater comparison between montane and flatland-dwelling hyaenas, it would be advisable to conduct density surveys across both areas.

8.6. Interdisciplinarity

Fusing biological and social sciences produced a well-rounded and in-depth understanding of human-brown hyaena relationships. This approach was indispensable in defining management recommendations.

From a personal point of view, merging social and biological sciences felt natural and commonsensical throughout the entire process. Interdisciplinary work is often challenging because researchers must master methodologies, concepts, and writing styles from diverse academic disciplines that they may not have been exposed to previously (Marzano *et al.*, 2006). I have prior experience conducting research in both the biological and the social sciences, although some of the methodologies I employed were new to me, therefore neither discipline felt foreign. Uniting the two fields was a new experience but I had an established appreciation of interdisciplinarity in conservation management, and saw each field as one half of a whole from the onset.

Aside from providing me with an enhanced understanding of the topic, an interdisciplinary approach opened doors within the community. By conducting a large quantity of interviews, I became acquainted with people who could help facilitate my biological research. When I began interpreting my biological data, I referred back to interviewees for additional quantitative information about the area. It was a fluid

process throughout. Although the hyaenas could not tell me their stories in the same way community members could, by studying their behaviour I was able to grasp both sides of the human-brown hyaena narrative. This balanced perspective made me feel objective, yet deeply invested.

8.7. Conclusions

Brown hyaenas need farmland and farms need brown hyaenas. Unfortunately, it is not that simple. Brown hyaenas are often considered 'invisible' which renders protective qualities, especially in comparison to the more 'visible' and disliked leopard, but it can also mean that the species' value within the ecosystem is overlooked and underappreciated, and hyaenas are subjected to fears associated with witchcraft.

Relationships with predators, both positive and negative, largely rest within the human dimension (Dickman, 2010). Perceptions of hyaenas vary vastly between socio-economic groups and are fraught with misconceptions, fears, cultural beliefs, and a battle for power and control, which harks back to colonial times. Experiences of livestock depredation by brown hyaenas are more likely to be perceived than real. Evidence from scats collected in and around the Soutpansberg Mountains suggests that brown hyaenas are probably predominantly scavengers and secure much of their food from leopards.

Although data from GPS collars and camera traps suggest hyaenas avoid areas of high human activity, human-wildlife conflict, either aimed at brown hyaenas or at other species, is threatening brown hyaena survival on private land. Non-targeted threats such as snaring and road collisions are often disregarded, but in northern Limpopo Province where hyaenas prefer roads to non-roads and where socio-economic conditions associated with snaring are rife, hyaenas may be more vulnerable to these risks than targeted persecution. Montane environments such as the Soutpansberg Mountains offer a temporary shelter for hyaenas from human activity and host a healthy density of brown hyaenas, but in the long run, this will not be enough to meet the species' large spatial needs. If the local leopard population does not recover from

its severe anthropogenic-induced local decline (Williams *et al.*, in review-b), brown hyaenas, especially in mountainous environments and on non-protected land, will face repercussions. Human-brown hyaena relationships within southern Africa need to change across multiple socio-economic groups through proactive, tailored, and holistic approaches which consider the whole large carnivore guild, to ensure the species' survival.

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Appendix 1: Written consent form for semi-structured interviews

Human-brown hyaena relationships in Limpopo Province, South Africa:
a cultural, social, and ecological investigation

Consent form to participate in Katy Williams's PhD research project at Durham
University

Date.....

This declaration certifies that I (insert name) _____ give my full consent to participate in the research project conducted by Katy Williams, Durham University. I have understood the aims and objectives of the research project and treatment of the final data set. The nature of the research has been fully explained to me including my rights to remain anonymous and to withdraw from the research project at any time without further need for justification.

I (delete as appropriate) do/ do not give permission to use an audio recorder during interviews. I understand that this tool will only be used as a memory aid for the purposes of transcribing the written material and details concerning my identity will remain anonymous.

If you agreed to be audio recorded during the interviews, please state whether you would prefer your information to be destroyed after completion of the research project or whether it can be retained by the individual researcher for future research use. I (delete as appropriate) do/ do not want information to be destroyed.

Thank you for your participation and cooperation with the research project.

Appendix 2: Interview scripts

Groups A, B, and C

Date:	Interviewer:	Questionnaire no:
GPS coordinates:		

Groups asked	Section A: General details		
A,B,C	A1	Name:	Anonymous?
A,B,C	A2	Ethnic group / tribe / language:	
A,B,C	A3	Age at last birthday:	
A,B,C	A4	Sex:	
A,B,C	A5	How many years of schooling?	
A	A6	Farm / business name:	
A,B,C	A7	Profession:	
A,B,C	A8	Main use of land:	
		Other uses:	
A	A9	For game farms - How do you use your game? (e.g. trophy hunting, photographic tourism, game meat, private use, scientific research, other)	
A,B,C	A10	On this property are you an owner, a lessee, a manager or a tenant?	
A,B,C	A11	If not the owner, who is the owner?	
A,B,C	A12	Length of time on farm / in area:	
A,B,C	A13	Where originally from:	
A,B,C	A14	Did you work / live elsewhere?	

Groups asked	Section B: Farm details			
A,B,C	B1	How big is your farm?		
A,B,C	B2	How many animals do you keep?		
			Number	Breed / notes
		Cattle		
		Sheep		
		Goat		
		Horse		
		Donkey		
		Chicken		
		Goose		
		Dog		
		Cat		
			Game animals?	
A,B,C	B3	Is owning livestock important in your culture?		

		Why or why not?
A,B,C	B4	Do you refer to any animals on your farm individually by name?
		If yes, which ones and what are their names? What do these names mean?
A,B,C	B5	Do you give any wild animals names?
		If yes, tell me about the animals and why they are named.
A,B,C	B6	Do you feel closer to the named animals?
		If yes, how?

Groups asked	Section C: Predator details	
A,B,C	C1	Which predators do you encounter on your farm? How often? (visual / spoor / calls)
A,B,C	C2	During your time have the numbers of the above predators increased, decreased or remained stable?
A,B,C	C3	What explanation do you have for any changes in numbers?

Groups asked	Section D: Predation and conflicts	
A,B,C	D1	Do you lose livestock to predators?
A,B,C	D2	Rank the problem predators according to the level of problem they cause: (Rank 1 - biggest problem to 8 - least problem)
A,B,C	D3	How do you protect your livestock from predators?
A,B,C	D4	How many animals do you think you lose to predators on average per year? (number or %)
A,B,C	D5	What is the total cost of losses per year?
A,B,C	D6	During your time here has the problem with predators increased, decreased or remained the same?

Groups asked	Section E: Brown hyaenas							
A,B,C	E1	Do you have brown hyaenas on your property?						
A,B,C	E2	If yes, how do you know this? (tracks, scat, sightings, photographs, noise)						
A,B,C	E3	Do you observe brown hyaenas moving or living as a collective group or as individuals?						
A,B,C	E4	Please give details of all clearly memorable brown or spotted hyaena sightings in the table below:						
		Date	Species	Time	Location	LUT	Number	Behaviour
A,B,C	E5	How strongly do you like or dislike the following species?						
			Strongly like		Mildly like	Neutral	Mildly dislike	Strongly dislike
		Brown hyaenas						
		Spotted hyaenas						
A,B,C	E6	Why do you like or dislike hyaenas?						
A,B,C	E7	Are you scared of hyaenas? Please give more information.						
A,B,C	E8	How do you feel about sharing your land with brown hyaenas?						
A,B,C	E9	Do you think the number of brown hyaenas in the area is low, moderate or high?						
A,B,C	E10	In the past 10 years, do you think brown hyaena numbers are decreasing, increasing or remaining the same?						
A,B,C	E11	Why do you think this is?						

A,B,C	E12	Have brown hyaenas caused any livestock / game losses on your property?
		If so, describe each loss (date, time of day / night, type of animal, its age, cost of loss)
		How much of the income lost from predation is caused by brown hyaenas?
A,B,C	E13	Have you ever had to kill or remove a hyaena?
		If yes, how?
		How many hyaenas did you remove in the last year?
		If none in the last year, how many hyaenas did you remove in the last five years?
A,B,C	E14	Have any of your neighbours removed a hyaena?
		If yes, who?
A,B,C	E15	Do any of your neighbours have big problems with hyaenas?
		If yes, who?
A,B,C	E16	Have you ever contacted Nature Conservation for assistance with hyaenas?
A,B,C	E17	Has anyone hunted hyaenas on your property for sport?
		If yes, give details:
A,B,C	E18	In this area where do you think the brown hyaenas mainly live?
A,B,C	E19	On your farm would you like fewer, more, the same number, or no brown hyaenas? Why?
A,B,C	E20	Where would you like brown hyaenas to live?
A,B,C	E21	Does the hyaena have any cultural associations for you?
		If yes, what are they?
A,B,C		Do you believe that hyaenas are linked to witchcraft and magic?
		If yes, what are the links?
C	E22	Can witches transform into hyaenas?
		Can witches ride on hyaenas?
		Is there anything else witches use hyaenas for?
		Do you believe in witches?
		Why or why not?
A,B,C		Are hyaenas used in traditional medicine?
		If yes, how?
C	E23	Have you ever visited a traditional healer?
		How often do you go?
		What do you go for?
A,B,C	E24	Do you know any stories or proverbs about hyaenas?
		If yes, what are they?
A,B,C	E25	Do you know any songs about hyaenas?
		If yes, what are they?
A,B,C	E26	Do you know of any rituals or ceremonies that involve hyaenas or references to hyaenas?
		If yes, what are they?
A,B,C	E27	What do you call hyaenas in your language?
		Does this vary between spotted and brown hyaenas?
		Do you or people you know use the term 'wolf' to describe hyaenas?
		What do you think the term symbolises?

Groups asked	Section F: Connection and involvement with nature	
B,C	F1	Do you ever visit the mountain?
B,C	F2	Why or why not? What do you do there? When do you go?
B,C	F3	Do you ever hunt in the mountain or elsewhere?
		If yes, how often?
		What do you hunt?
		How do you hunt?
		Do you hunt for sport or food?
B,C	F4	What resources do you or other people get from the mountain?
B,C	F5	How important is the mountain for you? Think in terms of animals, resources, history and emotional connections.
B,C	F6	If you went away, how did you feel when you returned to Buysdorp in relation to increased exposure to nature?

Group D

Date:	Interviewer:	Questionnaire no:
GPS coordinates:		

Section A: General details		
A1	Name:	Anonymous?
A2	Ethnic group / tribe / language:	
A3	Age at last birthday:	
A4	Sex:	
A5	How many years of schooling did you complete?	
A6	Length of time in area:	
A7	Where originally from:	
A8	Did you work / live elsewhere?	
A9	What did you do before you became a traditional healer?	

Section B: Traditional healing	
B1	Why did you become a traditional healer?
B2	How did you train to be a traditional healer?
B3	How long did it take to train to become a traditional healer?
B4	What skills do you need?
B5	How do you communicate with the ancestors?
B4	Do you get many customers?
	Is someone coming to see you every day for your services?
B5	How much do people pay for your services?

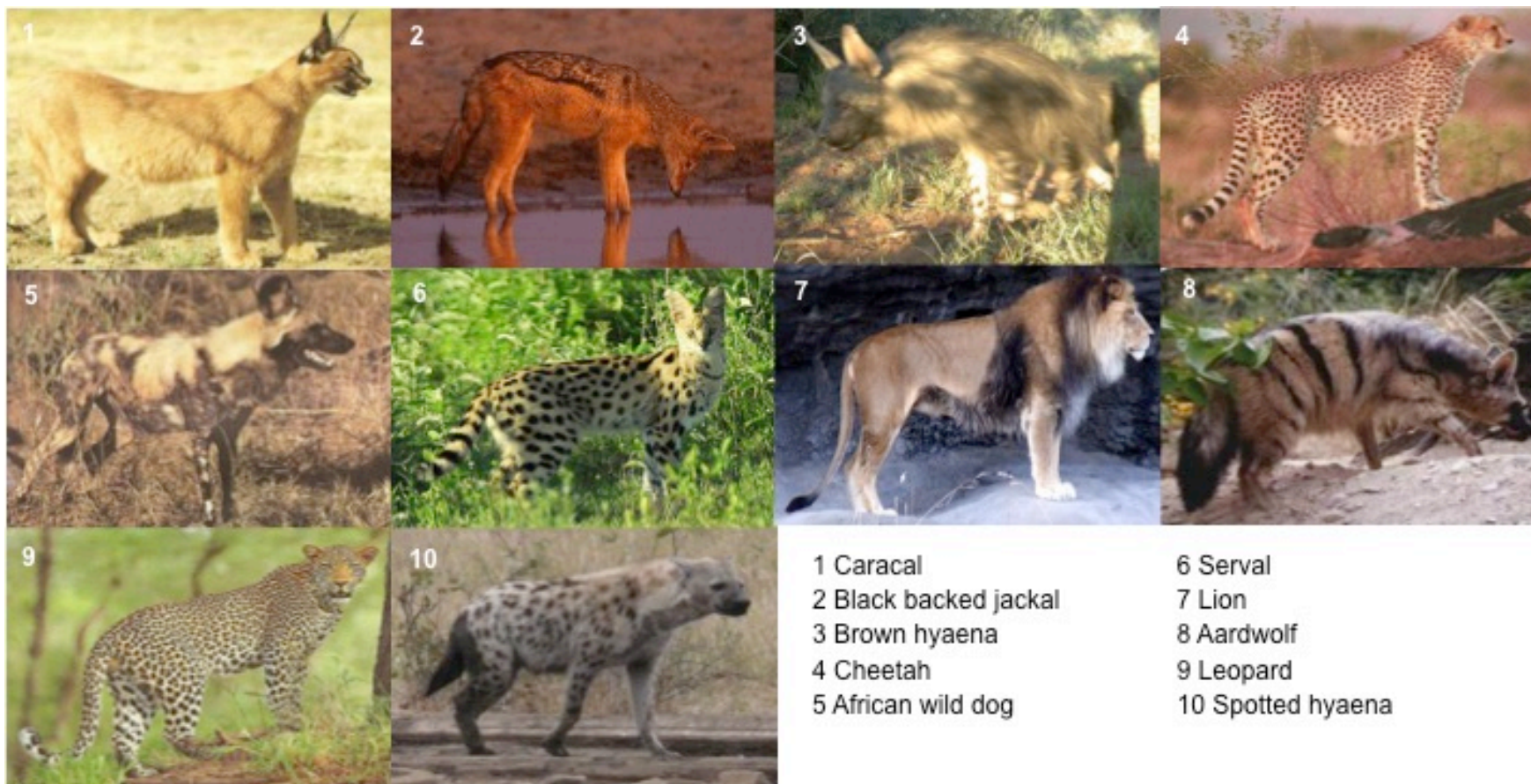
Section C: Natural resource usage	
C1	Do you use plant and animal products in your medicine?
	Which are the most powerful / important animals? Why?
C2	Are any specific animal body parts useful for different illnesses? Please provide examples.
C3	How do you prepare the medicines?
C4	What animals / objects are used in your bone bag?

	Why were they chosen?
C5	Do you feel a connection with nature?
	If yes, why?
C6	How do you feel about using wild animals for medicine? Especially in regards to animals that are endangered?

Section D: Brown hyaenas						
D1	Do you use hyaena and specifically brown hyaena body parts in your medicine?					
	If yes - how?					
D2	Are any specific hyaena body parts useful for different illnesses or problems? Give examples.					
D3	Do you use brown and spotted hyaena parts?					
	Is there are a difference in the power level between the two species?					
	Is the brown hyaena or the spotted hyaena more commonly used in traditional medicine in this area?					
D4	Where do you get hyaena body parts from?					
	How much do these parts cost?					
	Is the price increasing, decreasing or remaining the same? Why?					
D5	Is medicine using hyaena parts in demand?					
D6	How strongly do you like or dislike the following species?					
		Strongly like	Mildly like	Neutral	Mildly dislike	Strongly dislike
	Brown hyaenas					
	Spotted hyaenas					
D7	Why do you like or dislike hyaenas?					
D8	Does the hyaena have any cultural associations for you?					
	If yes what are they?					
	Is the hyaena considered a good animal or a bad animal? Is it associated with evil?					
D9	Do you believe that hyaenas are linked to witchcraft and magic?					
	If yes what are the links?					
	Can witches transform into hyaenas?					
	Can witches ride on hyaenas?					
	Is there anything else witches use hyaenas for?					
	Do you believe in witches?					
	Why or why not?					
	Are there many witches in your community?					
	How can they be identified?					
D10	Do you know any stories or proverbs about hyaenas?					
	If yes what are they?					
D11	Do you know any songs about hyaenas?					
	If yes what are they?					
D12	Do you know of any rituals or ceremonies that involve hyaenas or references to hyaenas?					
	If yes what are they?					
D13	What do you call hyaenas in your language?					
	Does this vary between spotted and brown hyaenas?					
	Do you or people you know use the term 'wolf' to describe hyaenas?					
	What do you think the term symbolises?					
D14	Have you ever seen a brown hyaena in the wild alive?					
	If yes, how did you feel?					

	Can you feel the power from the animal when it is alive as well as when it is dead?
--	---

Appendix 3: Predator identification photographs



Appendix 4: Questionnaire for landowners involved in the occupancy camera trapping survey

Camera trapping questionnaire

Thank you so much for allowing me to place a camera trap on your land. I really appreciate it and will ensure that you receive a DVD of all the photos taken there at the end of my study. I will also send you a copy of my thesis when it is finished so you can see my findings.

Please can you complete the following questions to help me understand the factors influencing the photos I take? Your answers are confidential so please do not feel afraid to tell the truth. Your name and property's name will not be mentioned in my report. Thank you.

1. Please place an x for the land uses on the property where my camera placed.

Land use	X for if this activity occurs
Livestock farming and breeding	
Agricultural farming	
Game farming and breeding	
Trophy hunting	
Eco-tourism	
Scientific research	
Private use	

2. Which of the above land uses are your main use/uses?

3. How big is the property where the camera is placed?

4. Which of the following animals do you keep and how many? If you don't know the number, please just estimate.

Animal	Number	Breed/optional notes
Cattle		
Sheep		
Goat		
Horse		
Donkey		
Chicken		
Dog		
Cat		
<i>Sable</i>		
<i>Giraffe</i>		
<i>Kudu</i>		
<i>Impala</i>		
<i>Blesbok</i>		
<i>Eland</i>		
<i>Gemsbok</i>		
<i>Waterbuck</i>		
<i>Wildebeest</i>		
<i>Red hartebeest</i>		
<i>Zebra</i>		
<i>Springbok</i>		

5. Which of the following predators do you have on your land?

Predator	Make an X if this animal occurs here	Notes on this animal's presence on your land – e.g. do you lose livestock or game to these animals? What impact does this have for you? How often do you see these animals?
Leopard		
Lion		
Cheetah		
Caracal		
Serval		
Wild dog		
Spotted hyena		

Brown hyena		
Aardwolf		

6. Have brown hyenas caused any livestock or game losses on your property?

Yes/No

If yes, describe the losses unless you have already described this in the previous question.

7. Have you ever had to kill or remove a problem brown hyena? Yes/No

If yes, how did you kill or remove the animals?

How many brown hyenas did you kill in the last year?

If none in the last year, how many brown hyenas did you kill in the last five years?

8. Has anyone hunted brown hyena on your property for sport/trophy hunting?

Yes/No

If yes, how many are killed a year?

9. How strongly do you like or dislike the following species?

	Strongly like	Mildly like	Neutral	Mildly dislike	Strongly dislike
Brown hyenas					
Spotted hyenas					

10. Please provide any additional comments on your relationships with predators or brown hyenas here.

11. Finally, in August 2014 I will be producing an exhibit of the best animal photos from this camera trapping survey which will be printed and publicly displayed in local towns to inform the public about the biodiversity of the area and promote nature conservation.

Can I use photos taken of wild animals on your property for the exhibit? Your name, your property's name and its location **will not** be revealed. Yes/No

Do you have any exceptions to this? E.g. you can use all photos taken except for ones of this species.

Appendix 5: Site covariates in occupancy analysis and their relationship to hypotheses

Covariate name	Covariate description	Testing hypotheses (Table 5.1)
Species richness (No of species per station including livestock)	A count of the number of species per station including livestock species; excluding humans and non-ground bird species diversity	5.1
Species richness (No of species per station)	A count of the number of species per station excluding livestock species, humans, and non-ground bird species diversity	5.1
Wild mammal richness	A count of the number of species per station excluding livestock species, humans, domestic dogs, and all bird species diversity	5.1
RAI Cow	RAI for cow captures	5.4
RAI Domestic Dog	RAI for domestic dog captures	5.3
RAI Donkey	RAI for donkey captures	5.4
RAI Goat	RAI for goat captures	5.4
RAI Horse	RAI for horse captures	5.4
RAI Human	RAI for human captures	5.3
RAI Leopard	RAI for leopard captures	5.2
RAI Sheep	RAI for sheep captures	5.4
RAI Spotted Hyaena	RAI for spotted hyaena captures	5.2
RAI Vehicle	RAI for vehicle captures	5.3

Covariate name	Covariate description	Testing hypotheses (Table 5.1)
RAI Antelope	RAI for all antelope captures (sums RAI estimates for bushbuck, common duiker, eland, gemsbok, greater kudu, impala, klipspringer, nyala, red duiker, Sharpe's grysbok, springbok, and steenbok)	5.1
RAI All Birds	RAI for all bird captures (sums RAI estimates for all bird species)	5.1
RAI Carnivores	RAI for all carnivore captures (sums RAI estimates for aardwolf, African civet, African wild cat, banded mongoose, bat-eared fox, black-backed jackal, caracal, dwarf mongoose, honey badger, large spotted genet, leopard, Selous' mongoose, side-striped jackal, slender mongoose, small spotted genet, spotted hyaena, striped polecat, water mongoose, and wild dog)	5.2
RAI Livestock	RAI for all livestock captures (sums RAI estimates for cow, donkey, goat, and sheep)	5.1, 5.4
RAI Large Carnivores	RAI for all large carnivores with an average female weight of 20 kg or greater (sums RAI estimates for leopard, spotted hyaena, and wild dog)	5.2
Total RAI per station	Sums RAI estimates per station	5.1
Total RAI per station human activity	Sums RAI estimates related to human activity per station (includes RAI domestic dog, RAI human, and RAI vehicle)	5.3
Total RAI per station human activity plus domestic animals	Sums RAI estimates related to human activity per station (includes RAI cow, RAI domestic dog, RAI donkey, RAI goat, RAI human, RAI horse, RAI sheep, and RAI vehicle)	5.3, 5.4
Total RAI per station wild activity	Total RAI per station - Total RAI per station human activity plus domestic animals	5.1
RAI Very small prey	Sums RAI for all prey species with an average female weight below 1 kg	5.1
RAI Small prey	Sums RAI for all prey species with an average female weight between 1 kg and 15 kg	5.1
RAI Medium prey	Sums RAI for all prey species with an average female weight between 15 kg and 50 kg	5.1
RAI Large prey	Sums RAI for all prey species with an average female weight 50 kg or greater	5.1
BAI Cow	BAI for cow captures	5.4

Covariate name	Covariate description	Testing hypotheses (Table 5.1)
BAI Donkey	BAI for donkey captures	5.4
BAI Antelope	BAI for all antelope captures (sums BAI estimates for bushbuck, common duiker, eland, gemsbok, greater kudu, impala, klipspringer, nyala, red duiker, Sharpe's grysbok, springbok, and steenbok)	5.1
BAI All Birds	BAI for all bird captures (sums BAI estimates for all bird species)	5.1
BAI Carnivores	BAI for all carnivore captures (sums BAI estimates for aardwolf, African civet, African wild cat, banded mongoose, bat-eared fox, black-backed jackal, caracal, dwarf mongoose, honey badger, large spotted genet, leopard, Selous' mongoose, side-striped jackal, slender mongoose, small spotted genet, spotted hyaena, striped polecat, water mongoose, and wild dog)	5.2
BAI Livestock	BAI for all livestock captures (sums BAI estimates for cow, donkey, goat and sheep)	5.1, 5.4
BAI Large Carnivores	BAI for all large carnivores with an average female weight of 20 kg or greater (sums BAI estimates for leopard, spotted hyaena, and wild dog)	5.2
Total BAI per station	Sums BAI estimates per station	5.1
BAI Very small prey	Sums BAI for all prey species with an average female weight below 1 kg	5.1
BAI Small prey	Sums BAI for all prey species with an average female weight between 1 kg and 15 kg	5.1
BAI Medium prey	Sums BAI for all prey species with an average female weight between 15 kg and 50 kg	5.1
BAI Large prey	Sums BAI for all prey species with an average female weight 50 kg or greater	5.1
Habitat thickness	Stations categorised into Open (mostly grassland), Mix (woodland/grassland mix), and Closed (mostly woodland)	5.7
Altitude	Altitude at each station	5.8
Area	Stations categorised into Limpopo Valley, Soutpansberg Mountains, and lowveld	5.8

Covariate name	Covariate description	Testing hypotheses (Table 5.1)
Fence	Stations categorised by fence type on the property (Game fence, Cattle fence, No fence)	5.6
Fence Electrified	Fence electrified (Yes, No)	5.6
Game farming	Game farming at site (Yes, No)	5.5, 5.6
Livestock farming	Livestock farming at site (Yes, No)	5.4, 5.5
Agricultural/plantation farming	Agricultural/plantation farming at site (Yes, No)	5.5, 5.6
Size of property	Size of property in hectares	5.5
Acceptance level for BH	Scaled based on landowner's acceptance level towards brown hyaenas (1 strongly dislike, 2 mildly dislike, 3 neutral, 4 mildly like, 5 strongly like)	5.3
Kill BH/BH problem animal	Brown hyaenas killed on the property for being a problem animal (Yes, No)	5.3
Camera on fenceline	Camera trap placed along fenceline (Yes, No)	5.6

Appendix 6: Non-domesticated mammal species photographed during the occupancy camera trapping survey

Common name	Latin name	Taxonomic order
Aardvark	<i>Orycteropus afer</i>	Tubulidentata
Aardwolf	<i>Proteles cristatus</i>	Carnivora
African civet	<i>Civettictis civetta</i>	Carnivora
African wild cat	<i>Felis silverstris</i>	Carnivora
African wild dog	<i>Lycaon pictus</i>	Carnivora
Banded mongoose	<i>Mungos mungo</i>	Carnivora
Bat-eared fox	<i>Otocyon megalotis</i>	Carnivora
Black-backed jackal	<i>Canis mesomelas</i>	Carnivora
Blue wildebeest	<i>Connochaetes taurinus</i>	Cetartiodactyla
Brown hyaena	<i>Hyaena brunnea</i>	Carnivora
Bushbuck	<i>Tragelaphus scriptus</i>	Cetartiodactyla
Bushpig	<i>Potamochoerus larvatus</i>	Cetartiodactyla
Cape porcupine	<i>Hystrix africaeaustralis</i>	Rodentia
Caracal	<i>Caracal caracal</i>	Carnivora
Chacma baboon	<i>Papio ursinus</i>	Primates
Common duiker	<i>Sylvicapra grimmia</i>	Cetartiodactyla
Common warthog	<i>Phacochoerus africanus</i>	Cetartiodactyla
Dwarf mongoose	<i>Helogale parvula</i>	Carnivora
Eland	<i>Tragelaphus oryx</i>	Cetartiodactyla
Gemsbok	<i>Oryx gazella</i>	Cetartiodactyla
Giraffe	<i>Giraffa camelopardalis</i>	Cetartiodactyla
Greater cane rat	<i>Thryonomys swinderianus</i>	Rodentia
Greater kudu	<i>Tragelaphus strepsiceros</i>	Cetartiodactyla
Honey badger	<i>Mellivora capensis</i>	Carnivora
Impala	<i>Aepyceros melampus</i>	Cetartiodactyla
Jameson's red rock rabbit	<i>Pronolagus randensis</i>	Lagomorpha
Klipspringer	<i>Oreotragus oreotragus</i>	Cetartiodactyla
Large spotted genet	<i>Genetta tigrina</i>	Carnivora
Leopard	<i>Panthera pardus</i>	Carnivora
Lesser bushbaby	<i>Galago senegalensis</i>	Primates
Mouse	*	Rodentia

Common name	Latin name	Taxonomic order
Nyala	<i>Tragelaphus angasii</i>	Cetartiodactyla
Red duiker	<i>Cephalophus natalensis</i>	Cetartiodactyla
Samango monkey	<i>Cercopithecus albogularis</i>	Primates
Scrub hare	<i>Lepus saxatilis</i>	Lagomorpha
Selous' mongoose	<i>Paracynictis selousi</i>	Carnivora
Serval	<i>Leptailurus serval</i>	Carnivora
Sharpe's grysbok	<i>Raphicerus sharpei</i>	Cetartiodactyla
Side-striped jackal	<i>Canis adustus</i>	Carnivora
Slender mongoose	<i>Galerella sanguinea</i>	Carnivora
Small spotted genet	<i>Genetta genetta</i>	Carnivora
Spotted hyaena	<i>Crocuta crocuta</i>	Carnivora
Springbok	<i>Antidorcas marsupialis</i>	Cetartiodactyla
Steenbok	<i>Raphicerus campestris</i>	Cetartiodactyla
Striped polecat	<i>Ictonyx striatus</i>	Carnivora
Thick-tailed bushbaby	<i>Otolemur crassicaudatus</i>	Primates
Tree squirrel	<i>Paraxerus cepapi</i>	Rodentia
Vervet monkey	<i>Chlorocebus pygerythrus</i>	Primates
White rhinoceros	<i>Ceratotherium simum</i>	Perissodactyla
Zebra	<i>Equus burchelli</i>	Perissodactyla

* Unidentifiable to species level

Appendix 7: Williams, K.S., Williams, S.T., Cilliers, N., Fitzgerald, L.E., Sheppard, E.C., Bell, S. and Hill, R.A. (in review) Large carnivores as socioecological keystone species. Biodiversity and Conservation.

Large carnivores as socioecological keystone species

Kathryn S. Williams ^{a,b*}, Samuel T. Williams ^{a,b,c}, Noeks Cilliers ^b, Leanne E. Fitzgerald ^{a,b}, Eleanor C. Sheppard ^b, Sandra Bell ^a, and Russell A. Hill ^{a,b}

^a Department of Anthropology, Durham University, Dawson Building, South Road, Durham, DH1 3LE, UK

^b Primate and Predator Project, Lajuma Research Centre, PO Box 522, Makhado 0920, South Africa

^c Department of Biodiversity, University of Limpopo, PO Box X1106, Sovenga, 0727, South Africa

*Corresponding author: Kathryn S. Williams (k.s.williams@durham.ac.uk), +27 (0) 710559557

Abstract

The surrogate species framework was developed to improve the efficiency of conservation programmes. However, it has not been utilised to mitigate anthropogenic impacts on wildlife, which are emerging as drivers of the global extinction crisis. We applied one aspect of the surrogate species framework, the keystone species concept, within ecological and social contexts, using large carnivores in the Soutpansberg Mountains, South Africa, as a case study. We used scat analysis to determine dietary composition and dietary overlap of brown hyaenas (*Hyaena brunnea*) and leopards (*Panthera pardus*), and to explore the role of leopards as ecological keystone species by providing scavenging opportunities for brown hyaenas. We used interviews to assess perceptions and attitudes towards large carnivores on private land. Interview data investigated the role of leopards as cultural keystone species that mitigate conflict between humans and brown hyaenas. There was significant overlap between the two species' diets. Food consumed by brown hyaenas was most likely acquired through scavenging, primarily from leopards. Livestock accounted for 9.91% of brown hyaena dietary occurrences. No leopard scats contained livestock yet leopards were perceived to be the most problematic predator. Brown hyaenas were blamed for livestock losses less frequently; the brown hyaena's secretive nature and participants' hatred towards leopards appeared to protect them from much negative attention. We argue that leopards act as socioecological keystone species, and benefit brown hyaena conservation by providing carrion and shielding them from persecution. Extending the surrogate species concept to encapsulate social dimensions provides a more holistic framework to conserve wildlife.

Key Words Surrogate species · Brown hyaena · Leopard · Diet · Human-wildlife conflict · Conservation

Introduction

Conservation biologists developed the surrogate species concept as a tool to facilitate more efficient conservation planning (Favreau et al. 2006). The central tenet of the surrogate species concept is that conserving certain species can provide protection to a much broader community of species (Jones et al. 2016). This allows surveys and conservation initiatives to be targeted at designated species rather than entire biological communities, reducing the cost, time, and effort required to survey habitats and implement conservation programmes (Favreau et al. 2006). There are several types of surrogate species, such as keystone species and flagship species. Keystone species have disproportionately large impacts on their ecosystems or processes than would be predicted based on their biomass (Simberloff 1998). Flagship species serve as symbols to raise awareness, support, and funds for conservation due to their charisma and public appeal (Heywood and Watson 1995). Although the surrogate species approach has been criticised (Linnell et al. 2000; Roberge and Angelstam 2004), it can be effective (Branton and Richardson 2011; Olds et al. 2014; Sergio et al. 2006; Thornton et al. 2016) and remains widely used in conservation planning (Jones et al. 2016; Thornton et al. 2016).

Some aspects of the surrogate species concept, such as flagship species, emphasise the role of the human dimension in biodiversity conservation (Thomas-Walters and Raihani 2016). One of the surrogate species concepts, keystone species, has been applied to the social sciences; cultural keystone species have been identified as those that have

exceptional cultural significance, for example providing medicine, food, or raw materials (Garibaldi and Turner 2004). This describes how wildlife enriches human culture, but the surrogate species concept has yet to fully exploit the social sciences in order to benefit wildlife conservation. Here we apply the keystone species concept in both ecological and social frameworks and combine them into a socioecological paradigm, using the large carnivore guild outside of protected areas in the Soutpansberg Mountains, South Africa, as a case study.

One way in which the surrogate species concept can be applied in large carnivore conservation relates to how scavengers depend on other large carnivores to kill prey species that can be incorporated into their diet through kleptoparasitism (Wilmers et al. 2003; Yarnell et al. 2013). The brown hyaena (*Hyaena brunnea*; near threatened on the IUCN Red List of Threatened Species (Wiesel 2015)) for example, is a poor hunter, and typically depends on scavenging to meet approximately 95% of its dietary intake (Maude and Mills 2005; Mills 1984; Owens and Owens 1978). It therefore relies heavily on other large carnivores such as the leopard (*Panthera pardus*; vulnerable on the IUCN Red List of Threatened Species (Stein et al. 2015a)) to kill prey species (Mills 2015; Slater and Muller 2014; Stein et al. 2013). After feeding, predators such as leopards often become satiated before they can completely consume large prey animals, so they leave and return to the kill on subsequent occasions to feed further, providing ample scavenging opportunities (Karanth and Sunquist 2000; Stein et al. 2013). In areas devoid of other large carnivores, leopards are less likely to hoist kills in trees (Stein et al. 2015b; Stein et al. 2013), therefore enabling greater scavenging possibilities for brown hyaenas. Hyaenas are adapted to exploit the remains of carcasses that cannot be utilised by other carnivores, such as bones and skin (Mills 1990). Their strong jaws

crush bones and hydrochloric acids in the gut aid digestion (Estes 1991; Mills 1990; Sutcliffe 1970).

Brown hyaenas, and many other scavengers such as vultures (Family: Accipitridae) (Yarnell et al. 2014) and hundreds of species of arthropods (Phylum: Arthropoda) (Jones et al. 2015), are thus likely to depend on large carnivores as keystone species to provide carrion. The degree of dietary overlap between brown hyaenas and large carnivores such as leopards and lions (*Panthera leo*), however, has rarely been assessed. If there is a high degree of dietary overlap, then framing conservation efforts to protect large carnivores as keystone species to benefit the conservation of scavengers such as brown hyaenas would be justified. This would complement the use of leopards and lions as flagship species, which are much more likely to attract favourable public attention than hyaenas (Van der Meer et al. 2016).

In addition to the traditional ecological context, we argue that the keystone species concept can also be applied to carnivore conservation in a sociocultural framework, such as in relation to human-wildlife conflict. Human-wildlife conflict is one of the key drivers of drastic global declines in carnivore populations (Ripple et al. 2016), and it also threatens human physical wellbeing and economic livelihoods (Thirgood et al. 2005). Conflict between humans and carnivores primarily occurs when predators cause or are believed to cause human fatalities or injuries (Liu et al. 2011; Packer et al. 2005) or depredation of livestock or game (Ogada et al. 2003; Thorn et al. 2012), leading to persecution of carnivores (Inskip and Zimmermann 2009). Lethal retaliatory behaviour against carnivores blamed for livestock and game losses is common, especially by people with negative attitudes towards the problem animals or experiencing regular

losses (Romañach et al. 2011). Indirect human-induced threats such as snaring for bush meat, secondary poisoning, and road collisions also endanger predators (Becker et al. 2013; Grilo et al. 2009; St John et al. 2011).

While some large carnivores such as lions are largely confined to protected areas, others have substantial portions of their range outside of protected areas. Protected areas are extremely important for carnivore conservation but in Africa these areas are not large enough to meet the spatial needs of large mammals (Mills 2005; Woodroffe and Ginsberg 1998), or sufficient to protect species such as brown hyaenas which thrive in the absence of competitor species like spotted hyaenas (*Crocuta crocuta*) (Mills 1984). Large predators such as lions, spotted hyaenas, cheetahs (*Acinonyx jubatus*), and African wild dogs (*Lycaon pictus*) have been largely extirpated from much unprotected land in southern Africa (Ray et al. 2005). The absence of these species leaves leopards and brown hyaenas as the apex predators across much of their range. Private land used for farming comprises a large proportion of the brown hyaena range, and is vital to their survival (Kent and Hill 2013; Maude and Mills 2005; Thorn et al. 2012). Approximately 83% of the extant leopard range is outside of protected areas (Jacobson et al. 2016).

Carnivores occurring outside of protected areas are particularly vulnerable to anthropogenic threats. Human-wildlife conflict, especially outside of protected areas, is often complex; it can mask socio-economic issues (Dickman 2010), represent legacies of historical inequalities (Rust et al. 2016), or mistakenly attribute blame to species that are not responsible (Gusset et al. 2009; Maude and Mills 2005). Approaches that incorporate multiple disciplines are vital to unravel the intricacies of human-wildlife

conflict and to plan appropriate conservation strategies (Clark et al. 2001; Madden and McQuinn 2014). Despite gaining greater acknowledgement in recent years and many practitioners advocating this approach (Clark et al. 2001; Madden and McQuinn 2014; West and Brockington 2006), interdisciplinary studies are still relatively uncommon in the conservation sciences.

In this paper we use a multi-method interdisciplinary approach to explore brown hyaena conservation using leopards as a socioecological keystone species. Through a biological investigation, we assess the dietary composition of brown hyaenas and leopards and the degree of dietary overlap between these species, allowing us to ascertain whether leopards act as an ecological keystone species and play a large role in providing scavengers with opportunities for kleptoparasitism. We also use social research techniques to ascertain the perceptions of owners and managers of private land towards predators, and their experiences of depredation, which enables us to assess the potential for leopards to act as sociocultural keystone species that benefit brown hyaena conservation by mitigating conflict between humans and brown hyaenas. By adopting an interdisciplinary approach, we extend the keystone species concept to develop a socioecological framework to benefit biodiversity conservation in which to construct a holistic understanding of intra-guild dependency and human-wildlife conflict.

Methods

Study site

Data were collected from private properties in and around the Soutpansberg Mountains, Limpopo Province, South Africa (Fig. 1). The Soutpansberg Mountains range in altitude from 200 m to 1,748 m above sea level and span approximately 210 km from east to west with a north-south width of up to 60 km at its widest point (Berger et al. 2003). Rainfall in the Soutpansberg Mountains ranges from 367 mm to over 2,000 mm per annum (Kabanda 2003). Versatile climatic conditions and the mountains' undulating topography produce a myriad of biomes which host an extremely high level of biodiversity (Macdonald et al. 2003). Much of the land in the mountains is unsuitable for farming and is used for leisure or ecotourism. Nearby low-lying areas to the north and south of the mountains, where rainfall levels are much lower (Davies-Mostert et al. 2013), are mainly used for livestock, game, and agricultural farming.

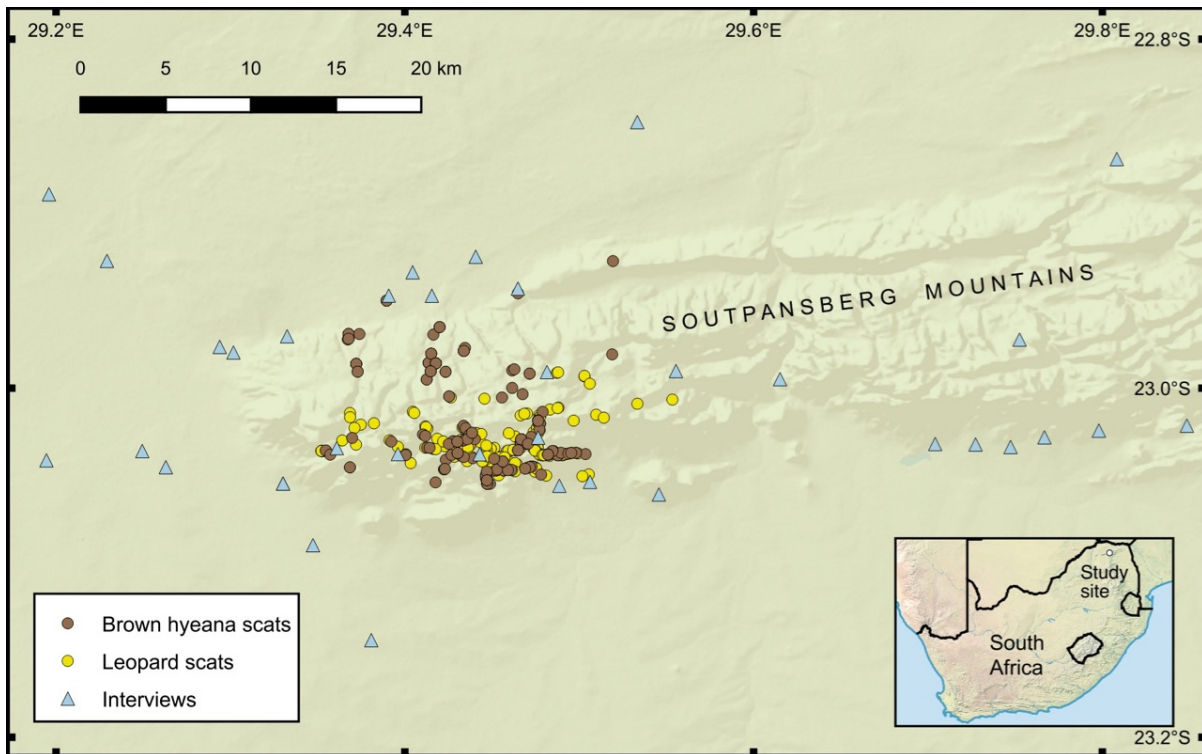


Fig. 1 Locations of scats collected and interviews conducted in and around the Soutpansberg Mountains, Limpopo Province, South Africa, between June 2011 and April 2016

Several communities live near the base of the mountains. Limpopo Province has the highest unemployment and the lowest average annual household income of the nine provinces in South Africa (Statistics South Africa 2012) and many residents in these communities suffer from poor economic conditions. Snaring for consumable bush meat or for leisure is thought to be common as a result, but little is known about this practice or its prevalence.

Within the mountains and the flatlands south of the mountains, leopards and brown hyaenas are the only resident large carnivores (Knott et al. 2003). Spotted hyaenas, cheetahs, and African wild dogs pass through these areas occasionally. North of the

Soutpansberg Mountains, the resident large carnivore guild is comprised of lions, cheetahs, leopards, African wild dogs, spotted hyaenas, and brown hyaenas.

Scat collection and analysis

Scats were collected opportunistically in the western Soutpansberg Mountains from wild brown hyaenas (n = 202 scats) and leopards (n = 237 scats) between June 2011 and April 2016. Careful consideration of identifying features such as colouration, size, and weight was employed to ensure that scats were correctly assigned to species. Scats were placed in a wire sieve with 1 mm sized mesh and washed in water to remove all faecal matter (Kuhn et al. 2008). Remaining organic material was sun-dried in trays. Dried contents were spread across a random sampling tray consisting of 36 or 100 numbered squares based on the size of the contents (Martins et al. 2011) and the contents' macroscopic qualities were noted. For all brown hyaena scats and 75 leopard scats, 40 hairs from every scat were selected at random – 20 were used for cuticular scale imprints (following Keogh 1983) and 20 were embedded in clear wax and cross-sectioned (following Douglas 1989). For the remaining 162 leopard scats, only cross-sectional analysis was conducted. Cuticular imprints and cross-sections were carefully examined under a standard light microscope at 40x – 100x magnification. The species from which hairs originated were identified by comparing samples with a reference library of hairs collected from known mammal species and with published guides (Keogh 1983; Seiler 2010; Taru and Backwell 2013). All samples were assessed a minimum of two times to ensure accuracy in the identification of contents.

All occurrences of a prey item within a scat were calculated as a relative frequency of occurrence and a corrected frequency of occurrence (Braczkowski et al. 2012; Henschel et al. 2005). Leopard diet was compared with brown hyaena diet for dietary overlap using the Pianka's index (Pianka 1973):

$$\alpha = \frac{\sum P_{ia}P_{ib}}{\sqrt{\sum P_{ia}^2 \sum P_{ib}^2}}$$

where α equals the dietary overlap between species a and species b , P_{ia} is corrected frequency of occurrence in species a , and P_{ib} is corrected frequency of occurrence in species b . Results range from 0 (no overlap) to 1 (complete overlap) (Pianka 1973) and values greater than 0.6 were deemed biologically significant (Navia et al. 2007).

The relationship between the corrected occurrence of species in leopard scats and the corrected occurrence of species in brown hyaena scats was further tested using linear regression in R v. 3.3.1 (R Development Core Team 2016). Since apex predators such as leopards frequently consume the entirety or the majority of a small sized carcass (Ackerman et al. 1984), analysis was limited to species with an average adult female weight greater than 15 kg. An arcsine square root transformation was applied to these data prior to analysis as recommended to meet the assumption of normal distribution for proportional data (Zar 2009).

Semi-structured interviews

Between April 2013 and February 2015, we conducted 36 semi-structured qualitative interviews with owners and managers of private properties in either English or

Afrikaans. Interviewees discussed 38 properties, totalling 735 km², which they either owned or managed. Properties were used for livestock farming (n = 6), game farming (n = 12), ecotourism (n = 6), or a combination of these uses (n = 14). We had an established rapport with many respondents prior to interviewing due to the Primate and Predator Project's presence in the area. Additional informants were recruited using snowball sampling (Browne 2005). Interviews took place in the respondents' homes or in a public place after we provided a comprehensive introduction to the research aims and gained informed consent. All interviewees were assured full confidentiality and anonymity to encourage open and honest dialogues pertaining to sensitive issues. Each interview lasted approximately 45 minutes. With the interviewee's permission, interviews were recorded using an audio recorder for transcription purposes. Afrikaans interviews were later translated into English. Interview transcripts were inputted into NVIVO v 10.2 (QSR International 2014) for theme identification and exploration. Themes were selected based upon inductive and *a priori* approaches (Ryan and Bernard 2003).

The interview script was primarily comprised of open-ended questions, but some closed questions were also included. During each interview, we collected information about respondents' personal characteristics and the properties they owned or managed. Their attitudes towards, knowledge pertaining to, and direct experiences of locally present predators were investigated. A five-point Likert scale (1 = strongly dislike, 2 = mildly dislike, 3 = neutral, 4 = mildly like, 5 = strongly like) was employed to examine attitudes towards brown hyaenas. We asked about conflict with large predators, with a focus on brown hyaenas. We gathered data on instances of conflict, extent of damage

by predators, preventative measures employed, and retaliatory killing of predators recently and historically.

Results

Dietary composition and overlap

Forty-four mammalian species were identified in brown hyaena scats and 24 mammalian species were detected in leopard scats (Table 1). Invertebrate remains were found in two brown hyaena scats. A wide variety of species were detected in brown hyaena scats (mean 1.95 species \pm 0.91 S.D.; range 1 – 5 species per scat). Individual leopard scats had lower species diversity in their contents (mean 1.40 species \pm 0.57 S.D.; range 1 – 3 species per scat). The five most frequently consumed species by brown hyaena were bushbuck, common warthog, chacma baboon, impala, and common duiker. Three of these species (bushbuck, chacma baboon, and common duiker) also ranked highest in the leopard diet. Bushbuck was the most commonly consumed prey item for both brown hyaenas and leopards. Livestock (cows, goats, and sheep) accounted for 9.91% of brown hyaena dietary occurrences. No livestock remains were detected in leopard scats. Dietary overlap between leopard and brown hyaena diet was biologically significant, with a Pianka's index of 0.739.

Table 1 Occurrence of mammalian prey species identified in brown hyaena and leopard scats collected in the western Soutpansberg Mountains, South Africa between June 2011 and April 2016. Prey size groupings are based on classifications by Mills and Mills (1978).

Prey species	Brown hyaena (n=202)		Leopard (n=237)	
	Corrected Occurrences	Corrected frequency of occurrence %	Corrected Occurrences	Corrected frequency of occurrence %
Large mammals (> 50 kg)				
Blesbok, <i>Damaliscus pygargus</i>	1.5	0.74		
Blue wildebeest, <i>Connochaetes taurinus</i>	1.17	0.58	0.33	0.14
Bushpig, <i>Potamochoerus larvatus</i>	12.58	6.23	24	10.13
Common warthog, <i>Phacochoerus africanus</i>	17.75	8.79	6.33	2.67
Gemsbok, <i>Oryx gazella</i>	3.83	1.9		
Giraffe, <i>Giraffa camelopardalis</i>	1	0.5		
Greater kudu, <i>Tragelaphus strepsiceros</i>	10.75	5.32	6	2.53
Nyala, <i>Tragelaphus angasii</i>	8.58	4.25	19.83	8.37
Sable, <i>Hippotragus niger</i>	1.33	0.66		
Waterbuck, <i>Kobus ellipsiprymnus</i>	3.25	1.61	4	1.69
Zebra, <i>Equus quagga</i>	2.58	1.28		
Domestic livestock				
Cow, <i>Bos taurus</i>	7	3.47		
Goat, <i>Capra aegagrus hircus</i>	11.25	5.57		
Sheep, <i>Ovis aries</i>	1.75	0.87		
Medium mammals (16 - 50 kg)				
Aardvark, <i>Orycteropus afer</i>	1.83	0.91		
Brown hyaena, <i>Hyaena brunnea</i>	1.92	0.95		
Bushbuck, <i>Tragelaphus scriptus</i>	24.17	11.96	80.83	34.11
Chacma baboon, <i>Papio ursinus</i>	17.17	8.5	16.83	7.1
Common duiker, <i>Sylvicapra grimmia</i>	13.33	6.6	15.67	6.61
Domestic dog, <i>Canis lupus familiaris</i>	0.5	0.25		
Grey rhebok, <i>Pelea capreolus</i>			1	0.42
Impala, <i>Aepyceros melampus</i>	13.75	6.81	3.83	1.62
Mountain reedbuck, <i>Redunca fulvorufula</i>			1.5	0.63
Small mammals (1 – 15 kg)				
African civet, <i>Civettictis civetta</i>	0.83	0.41		
Bat-eared fox, <i>Otocyon megalotis</i>	1	0.5		
Black-backed jackal, <i>Canis mesomelas</i>	1	0.5		
Cape porcupine, <i>Hystrix africaeaustralis</i>	0.67	0.33	5.17	2.18
Gambian giant rat, <i>Cricetomys gambianus</i>	1.25	0.62	1	0.42
Klipspringer, <i>Oreotragus oreotragus</i>	0.25	0.12	5.67	2.39
Large spotted genet, <i>Genetta maculata</i>	0.5	0.25		
Mongoose, Family: Herpestidae ^a	4.5	2.23		
Red duiker, <i>Cephalophus natalensis</i>	9.17	4.54	8.83	3.73
Rock dassie, <i>Procavia capensis</i>	1.33	0.66	12.17	5.13
Samango monkey, <i>Cercopithecus albogularis</i>	4.33	2.15	7	2.95
Sharpe's grysbok, <i>Raphicerus sharpei</i>	1	0.5		

Small spotted genet, <i>Genetta genetta</i>	0.33	0.17		
Steenbok, <i>Raphicerus campestris</i>	1	0.5		
Thick-Tailed Bushbaby, <i>Otolemur crassicaudatus</i>			1	0.42
Vervet monkey, <i>Chlorocebus pygerythrus</i>	6.42	3.18		
Yellow spotted dassie, <i>Heterohyrax brucei</i>	4.58	2.27	11.5	4.85
Very small mammals (< 1 kg)				
Four striped mouse, <i>Rhabdomys pumilio</i>	1.83	0.91	1	0.42
House rat, <i>Rattus rattus</i>	0.92	0.45		
Lesser bushbaby, <i>Galago moholi</i>	1	0.5		
Lesser red musk shrew, <i>Crocidura hirta</i>	0.75	0.37		
Namaqua rock mouse, <i>Aethomys namaquensis</i>			0.5	0.21
Red veld rat, <i>Aethomys chrysophilus</i>	0.25	0.12		
Rock elephant shrew, <i>Elephantulus myurus</i>	1.25	0.62	2	0.84
Swamp musk shrew, <i>Crocidura mariquensis</i>	0.83	0.41		
Woodland dormouse, <i>Graphiurus murinus</i>			0.5	0.21
Total		100		100

^a It was possible to identify mongooses only to a Family level.

There was a significant positive relationship between the corrected frequency of occurrence of medium and large species in leopard scats and in brown hyaena scats (linear regression: $R^2 = 0.489$, $F_{(1,21)} = 20.09$, $p = 0.0002$, gradient = 0.482, intercept = 0.111) (Fig.2).

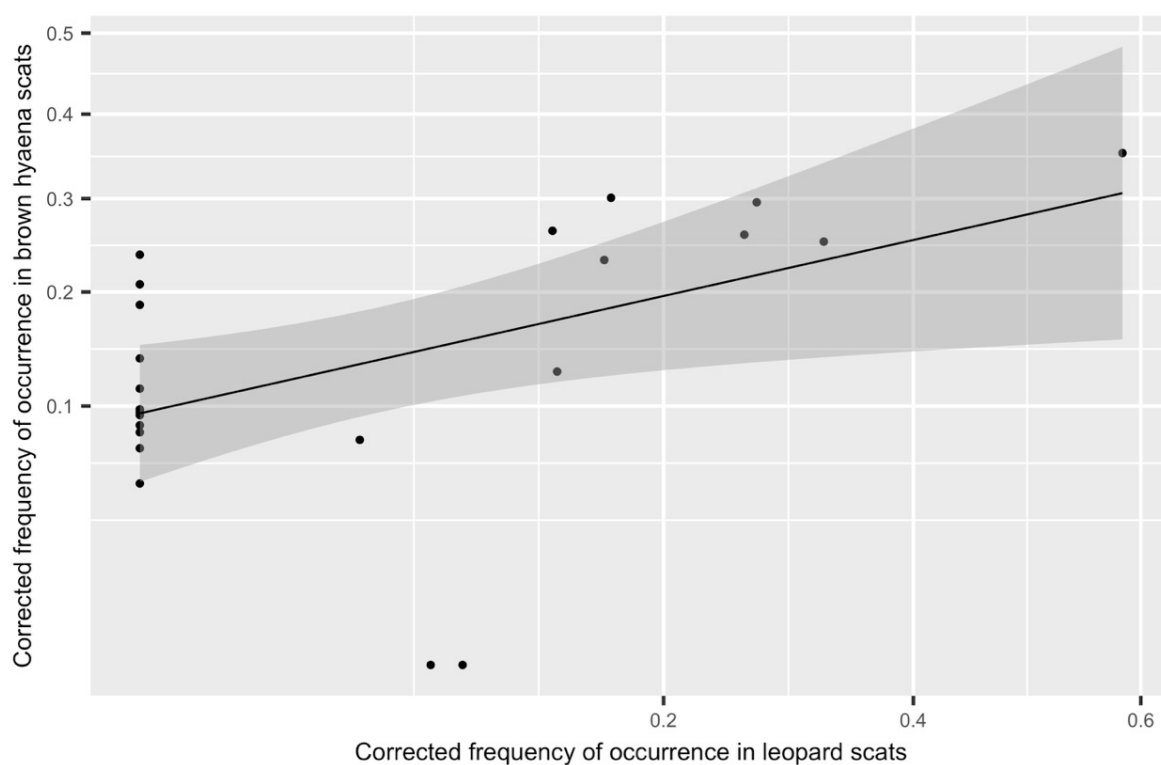


Fig.2 Transformed corrected frequency of medium (16 – 50 kg) and large (> 50 kg) species occurrence in brown hyaena scats against transformed corrected frequency of medium and large species occurrence in leopard scats. Scats were collected in the western Soutpansberg Mountains, South Africa between June 2011 and April 2016. Data was transformed using arcsine square root. Dark grey area represents the 95% confidence interval.

Attitudes and perceptions

Seventy-eight per cent of landowners or managers had seen a brown hyaena on their property at some point, although these sightings were extremely rare. The brown hyaena's elusive nature was often discussed as a positive and almost magical trait, causing several interviewees to refer to them as 'ghosts' or 'ghostlike':

I see them as ghosts. They really are. We call them ghosts because they are around but they are so unobservable and their ranging seems to be so wide. You hardly ever see the things, even though they are very present.

Overall, landowners and managers were tolerant towards the presence of brown hyaenas and other predators on their land if they displayed ‘acceptable’ behaviour and “*minded their p’s and q’s*”. The definition of acceptable behaviour was often assigned to an animal’s feeding and hunting practices, especially in relation to livestock or expensive game species, and was defined by people at an individual level. The point when a predator’s behaviour shifted from tolerable to intolerable was frequently dependent on a personal threshold regarding the extent of losses and the species involved. Many respondents perceived depredation of livestock or expensive game species as unacceptable and worthy of retaliation. Conversely, some landowners and managers, especially those employing preventative measures towards depredation of livestock or involved in ecotourism, were acceptant of predators regardless of their behaviour and either disregarded livestock or game losses or blamed themselves.

For many interviewees, the loss of livestock or valuable game symbolised a loss of control over their property. The process of depredation was compared to theft, as indicated in this quote:

I wouldn’t really care much but you know it’s always painful if you lose something...It’s like a thief coming to steal or break into your house you know. If you know who it is, you won’t like that person.

Thirty-two per cent of landowners or managers reported problems with brown hyaenas. Brown hyaenas were said to predate on cows, sheep, and goats. They were perceived to cause additional damage by killing calves as they emerged during birthing, breaking the legs of livestock, biting the tails off of livestock, and causing fatal infections in bite sites on calves. Problems with leopards were believed to be more commonplace and affected 58% of respondents. In comparison to leopard depredation, attacks by brown hyaenas were considered infrequent and the amount of damage caused was perceived to be low. Only one interviewee experiencing conflict ranked the brown hyaena as a more problematic animal than the leopard. Although leopards were considered very problematic, several respondents stated that the biggest threat to their game or livestock was ‘two legged predators’ or human poachers.

Depredation or the threat of depredation had severe, multi-faceted effects on farmers economically, socially, emotionally, and mentally. The cost of losing a cow calf (average cost of a weaned calf is ZAR 4,000 / USD 279) or an expensive game animal such as a sable (bulls can sell for up to ZAR 27 million / USD 1.9 million (Pitman et al. 2016)) can be devastating for farmers. Not only does the farmer lose the animal’s purchase or selling value, but also its future breeding potential. One livestock farmer described how he cannot afford any financial losses from depredation and therefore he feels like he is unable to leave his farm for extended periods because he must kraal his livestock daily to try and protect them from predators. His frustration and despair at his loss of freedom was voiced in this quote:

You know if the leopard would just, if just concentrated on impala or whatever, they could have one a week as far as I’m concerned. It wouldn’t bother me at all. But why must they take my calves?

Following a predation event, farmers will sometimes respond by killing predators in retaliation as a way to re-establish control. Despite a high overall tolerance level towards brown hyaenas (average Likert score of 3.79), 10 brown hyaenas were reportedly killed in response to depredation or the risk of depredation in the past five years.

Discussion

Our findings indicate that leopards act as socioecological keystone species in the Soutpansberg Mountains, South Africa, by enhancing the conservation of brown hyaenas through food provision and protection from persecution by humans. The leopard's role as a provider of food sources for brown hyaena is demonstrated by a high degree of dietary overlap between the two species. Although scat analysis does not definitively explain how prey remains were acquired (Mills and Mills 1978; Nilsen et al. 2012), the high degree of dietary overlap we observed suggests that brown hyaenas regularly scavenge from leopards. This is especially likely for medium and large bodied animals that occur frequently in the leopard diet such as bushbuck, which are unlikely to be completely consumed by leopards immediately after making the kill. A similar trend was found on farmlands in Namibia where the two species have a similar diet and brown hyaenas scavenged at 76% of monitored leopard kills (Stein et al. 2013).

The brown hyaena diet encompassed a broader diversity of prey species than the leopard diet, as is common among scavengers (Hayward 2006; Mills 2015). The prevalence of medium and large species (78% of feeding occurrences), along with the high diversity of species found per scat (Alam and Khan 2015), and the presence of

invertebrate remains in brown hyaena scats (van der Merwe et al. 2009) also support the hypothesis that brown hyaenas acquired the majority of their food through scavenging rather than hunting. This finding is supported by other studies using direct observations, which determined that hunting only constitutes roughly 5% of the brown hyaena diet (Maude and Mills 2005; Mills 1984; Owens and Owens 1978). Successful brown hyaena hunts are predominantly restricted to small and very small bodied species (Maude and Mills 2005; Mills and Mills 1978); these were found very infrequently in the analysed scats.

Of the species comprising the brown hyaena diet native species predominated, but a low incidence of feeding on domestic livestock was also noted (9.91% of occurrences). Livestock depredation by brown hyaenas is rare; despite the presence of livestock in the diet of collared brown hyaenas in Botswana, they were never observed hunting livestock (Maude and Mills 2005). When brown hyaenas do hunt domestic livestock this is often attributed to one individual rather than a whole clan (Skinner 1976; Weise et al. 2015). Despite frequent accusations of leopard depredation by farmers, no livestock remains were detected in leopard scats. The lack of livestock in leopard scats may be attributed to geography. Scats were primarily collected near the top of the mountains where livestock farming is uncommon (as confirmed by interviews). Leopards, and especially female leopards, often occupy smaller home ranges and travel shorter daily distances than brown hyaenas (Chase Grey 2011; Martins and Harris 2013; Swanepoel et al. 2016; Williams 2017), therefore reducing the likelihood of a montane-dwelling leopard encountering cattle and returning to a high altitude area to defecate within the digestion period. Leopards do occasionally attack livestock in the area (unpublished data), although this is probably a more infrequent occurrence than

perceived by farmers. Therefore, it is likely that brown hyaenas may have secured some livestock remains from leopards residing at lower altitudes or by scavenging the remains of livestock that died from other causes such as disease.

Despite the fact that livestock depredation by brown hyaenas is rare, several farmers indicated that brown hyaenas actively hunt their livestock and that some farmers retaliate with lethal persecution. It is likely that the majority of these reports indicate a discrepancy between perceptions of predators' diets and actual consumption. In Botswana, farmers believe that cheetahs consume expensive game species like springbok (*Antidorcas marsupialis*), but scat analysis revealed that cheetahs primarily consume more abundant and less commercially valuable species like greater kudu (Boast et al. 2016). Similarly, farmers in the Soutpansberg Mountains also report higher levels of lost livestock and expensive game than is represented in the leopard diet (Chase Grey et al. in press).

Incongruities between results from scat analysis and reports of depredation by leopards and brown hyaenas suggest that accusations of blame may not entirely reflect realities. Instead, conflict with predators may be concealing human-human issues (Delibes-Mateos 2016; Dickman 2010; Madden 2004) such as those stemming from disparities in power and control over land. Snaring by community members was cited as a problem for private landowners and managers, and is contributing to local declines in leopard and brown hyaena (Williams 2017; Williams et al. in review). Due to the secretive nature of snaring and the challenges of governing large properties, farmers may attribute losses caused by snaring to predators like leopards and invoke retaliatory actions in an attempt to assert control over the misconceived situation (Rust et al. 2016).

This represents one layer of human-human conflict disguising human-predator conflict, however there is also a deeper underlying layer driving snaring practices. Present day inequalities in access to employment, land ownership, and education stem from historical legacies of colonialism and apartheid, and create conditions conducive to snaring (Lindsey et al. 2013; Rust et al. 2016).

Ascribing expectations to predators about acceptable behaviour on private land is another approach to assume control. However, predators are unaware of human expectations and how these differ within their landscape. Therefore as they move through their environment, they can transition from being a ‘decent citizen’ to a ‘bad animal’ unknowingly (Arluke and Sanders 1996, p. 175). Interviewees ascribed anthropomorphic qualities to predators by expecting them to understand and adhere to human-defined rules of acceptable behaviour. This sets them up for failure and encourages conflict. Suggesting predators deliberately and maliciously deviate from expectations may be used to rationalise lethal retaliatory responses.

Brown hyaenas avoided much negative attention from farmers because of the severe animosity shown towards predators like leopards. Leopards were perceived to be guilty of displaying unacceptable behaviours such as depredation more frequently. Consequently, leopards buffered less conspicuous predators from farmers’ negative attention and probably persecution. Unintentional blindness towards brown hyaena behaviour mirrors the psychological condition whereby an observer cannot focus his attention on all aspects of a scenario and may consciously or unconsciously overlook the least important or least obvious (Mack 2003; Simons and Chabris 1999). The brown hyaena’s ‘invisibility’ provided it with additional protection since it is sighted less

frequently than leopard and in the eyes of landowners and managers, this invisibility gave hyaenas a value. This was especially true of an ecotourist operator who said that showing a client a brown hyaena was a more valuable experience than finding a leopard.

In this case study, leopards provide brown hyaenas with scavenging opportunities and protection from anthropogenic risks and thus function as a socioecological keystone species. This research represents the first attempt to apply the surrogate species concept within a social framework to assess how human culture can be exploited to benefit wildlife conservation. We recommend a holistic multi-species approach that protects large carnivore guilds rather than a single species approach. Broader approaches to conservation that encompass multiple species or even landscapes are becoming increasingly popular, such as the focal species paradigm (Lindenmayer et al. 2014), which utilises a suite of species, each of which is used to define various attributes in a landscape (Lambeck 1997).

The socioecological keystone species concept can be applied to the case study by protecting brown hyaenas (and many other species) through enhancing the conservation status of leopards outside of protected areas. For example, the density of leopards in the Soutpansberg Mountains is declining rapidly, with the population having declined by over 60% in less than 10 years (Williams et al. in review). If this trend continues and the socioecological keystone species is effectively removed we predict that in the absence of any other large carnivores brown hyaenas may be compelled to hunt more often (van der Merwe et al. 2009). By conserving leopards, therefore, the potential for brown hyaenas to become livestock predators could be avoided. Unlike leopards, which

are efficient ambush predators in thick montane environments (Balme et al. 2007), brown hyaenas may struggle to acquire sufficient food within the refuge of the Soutpansberg Mountains and may widen their foraging and hunting areas to include more low-lying areas where they can exploit anthropogenic food sources which are easier to access (Williams 2017). This will expose them to greater anthropogenic threats and if their prey includes livestock or expensive game species, they will demonstrate unacceptable behaviours more frequently. This will be exacerbated by no longer being protected from persecution by leopards, as in absence of more visible predators, brown hyaenas will be brought to the forefront of hostilities with farmers.

In the Soutpansberg Mountains, promoting non-lethal conflict mitigation techniques such as kraaling livestock and the use of livestock guarding dogs may improve the likelihood of acceptable behaviour by leopards occurring on private land, thus retaining the power in the hands of the landowner or manager. These non-lethal control methods are more cost effective and successful than lethal control methods (McManus et al. 2015; Treves et al. 2016). In addition to reducing conflict, utilising non-lethal predator control techniques may also push landowners and managers to take more responsibility and change their mentality, creating an environment where all predator behaviour is acceptable. We also advocate that greater public education on brown hyaena ecology, diet, and their value to the ecosystem is required to replace misconceptions about the species. Finally, we suggest that extending the surrogate species concepts and integrating this within a socioecological framework will provide conservationists with a more holistic approach to biodiversity conservation.

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Compliance with ethical standards

Conflict of interest

The authors declare that they have no conflict of interest

Ethical approval

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